

The Ecology of the Chironomidae (Diptera)
in a New Eutrophic Reservoir

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This thesis is entirely my own work and has at no time
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(R.S. OLDHAM)

ABSTRACT

The Ecology of the Chironomidae (Diptera) in a New Eutrophic Reservoir

Andrew Edward Brown

The successional changes in a new, lowland reservoir in Leicestershire, England, were investigated, with particular reference to larvae of the Chironomidae.

During the first four years major changes in water chemistry were the result of the different sources of water used to fill the reservoir and the release of nutrients from the inundated terrestrial vegetation. Phytoplankton populations showed erratic changes in species composition and standing crop during the first year of filling. Seasonal fluctuations, similar to those observed at other eutrophic reservoirs, occurred in subsequent years.

Chironomid species composition and temporal and spatial variation in the larval populations were investigated. Orthocladiinae larvae were particularly abundant in mats of algae in shallow water in the second year after filling commenced. This was probably the result of a stable water level, warm weather conditions and high nutrient concentrations. In the third year Chironomus plumosus and Polypedilum nubeculosum larvae were numerically dominant. Populations of these species declined the following year and Tanytarsus species predominated. Temporal changes of the fauna were influenced by climate and the filling regime of the reservoir. Chironomid larvae did not indicate any marked differences in water quality between the two arms of the reservoir. Populations were generally found to be contagiously distributed.

Chironomids in rainbow and brown trout diets were investigated during the first two fishing seasons. The species composition of larvae and pupae in the diets suggested different feeding zones for the two trout species. The behaviour of chironomid larvae and not their numerical abundance determines their occurrence in the diets.

The results from this study are discussed in relation to management of the reservoir. Due to the importance of chironomids in trout diet it may be beneficial to base stocking policy on a knowledge of the seasonal population fluctuations of the chironomids.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Introduction

Population growth and industrial expansion in the east Midlands have resulted in an increased demand for water. In 1970 Royal Assent was given for the creation of a pump storage reservoir in Leicestershire, formerly the county of Rutland, that would create the largest man-made reservoir in Britain. The dam was closed in January 1975 and filling from the natural catchment area began. In January 1976 the pumps supplying water to the reservoir from the rivers Nene and Welland were commissioned and pumping commenced. Water was first made available for consumption in Autumn 1977.

Although the primary objective of the reservoir construction was water supply, the 1973 Water Act gave Water Authorities responsibilities for developing water-based recreation. Picnic areas, footpaths, a nature reserve, sailing and fishing facilities have all been developed. The Anglian Water Authority was advised by Jones, Liverpool University, to develop the reservoir as a trout fishery. Stocking with brown trout (Salmo trutta L.) and rainbow trout (Salmo gairdneri Richardson) began in March 1975. The fishery was exceptional in two ways: it was created where no previous large lake or reservoir existed and was stocked with relatively large numbers of small trout after attempts had been made to exclude coarse fish.

In 1971 the Rutland Water Research Committee (formerly Empingham Reservoir Research Committee) was founded. Its aims are to facilitate exchange of information and to co-ordinate the multi-disciplinary research projects on the reservoir. Projects of a biological nature involve monitoring water chemistry and phytoplankton (Anglian Water Authority), benthic invertebrate surveys of feeder streams and reservoir (Leicester University and Leicester

Polytechnic) and the growth and diet of trout (Leicester Polytechnic and Anglian Water Authority). The main objective of these studies is to assess the biological development of the reservoir with a view to developing procedures for the management of water abstraction, fisheries, recreation and conservation.

The present study concentrates on the benthic invertebrate populations, particularly the Chironomidae, their ecology and inter-relationships with the trout population.

Literature Review

a) Colonization and development of benthic communities in new impoundments

As world demand for water has increased large numbers of storage reservoirs have been constructed in many countries. Reviews of successional changes in these reservoirs are available for the United States (Jenkin, 1965), Canada (Nursall, 1969), Russia (Zhadin and Gerd, 1961) and tropical countries (McLachlan, 1974).

The majority of reservoirs are created by impounding a river with subsequent flooding of the river valley. However, in areas where there are serious disadvantages in constructing dams across rivers, pump storage reservoirs have been developed, particularly in recent years. In these reservoirs the water is provided either by gravity feed or by pumping from distant rivers. Studies on the development of benthic fauna have been predominantly on impoundment reservoirs (for example Nursall, 1952; Mel'nikov and Lubyantsev, 1958; Sokolova, 1963; Aggus, 1971; McLachlan and McLachlan, 1971; Armitage, 1977). The author knows of no similar studies on pump storage reservoirs.

Morduchai-Boltovskoi (1961) proposes that the successional changes of the benthos in direct river impoundments fall into four stages. During the first stage there is an increase in the

relative abundance of the existing fauna in the old river bed. In the second stage a few dominant species such as Chironomus plumosus (L.) larvae become very numerous. During the third stage there is a decline in the relative abundance of these populations and the development of a more diverse fauna. After a period of years the fourth stage is characterised by a more stable community.

Stage 1 (Morduchai-Boltovskoi, 1961)

As might be expected rheophilous organisms present in the impounded river are the first to colonize the new inundated habitat but in a few months die out due to their inability to survive the lentic conditions (Nursall, 1952). Sokolova (1963) found that the most rheophilous animals in the old river course died out almost immediately after impoundment of the river. Settling of suspended material and oxygen deficiency were thought to be the limiting factors. Several species completed their life cycles in the reservoir but no new generation appeared. Initially all aquatic animals are concentrated on the former stream or river bed. Terrestrial invertebrates such as Enchytraeidae, Arachnida and earthworms are found in areas of flooded vegetation (Campbell, 1963; Armitage, 1977). These gradually disappear and are replaced by lotic organisms. ?

Stage 2

The Chironomidae, particularly Chironomus plumosus, are frequently the earliest and most rapid colonizers of new impoundments (Nursall, 1952; Sokolova, 1963; Fillion, 1967; Paterson and Fernando, 1970a; Kruglova, 1959; Cantrell, 1975). Morduchai-Boltovskoi (1961) and Lellack (1966) have suggested that the increase in population density of this species is associated with the food resources that become available during decomposition of the terrestrial vegetation. It is likely that other factors are also involved. Walshe (1948, 1950) has demonstrated the ability of Chironomus plumosus larvae to withstand the low oxygen concentrations which prevail under

these conditions. Roff (1977) presents evidence that dispersionary activity in Diptera is positively correlated with size. It would, thus, be expected that Chironomus plumosus adults, amongst the largest in the family, would reach new habitats before smaller species.

In Ladyburn Lough, a new reservoir in north England, McLachlan (1975) found Chironomus plumosus to be the first summer invader, building up large populations within a few months of egg laying. During the winter period Procladius choreus Meigen was found to colonize by active migration of the larvae, a much slower process. In the Barrier Reservoir, Alberta, Pentapedilum and oligochaetes were the predominant organisms two months after the reservoir was filled (Nursall, 1952). These were replaced by Chironomus as the decomposing terrestrial vegetation produced eutrophic conditions on the reservoir floor. As conditions reverted back to oligotrophy Tanytarsus became the predominant genus. Sokolova (1963) recorded Chironomus larvae reaching considerable biomass in the shallow water of the Mozhaisk Reservoir, Russia, in July, three months after filling. By the end of July the deepest parts of the reservoir had been colonized, predominantly by the early instars. The depth and type of sediment were found to be important in determining their distribution.

Stage 3

In the third stage of development of impounded reservoirs Chironomus plumosus larvae are replaced by a more diverse fauna, including species of Mollusca, Oligochaeta, Hirudinea, Trichoptera and Ephemeroptera. Field and laboratory investigations indicate that early successional changes in species composition of the Chironomidae are at least partly attributable to larval interactions (Cantrell, 1975). Early instars of C. plumosus are poor competitors and settlement is not successful if large numbers of other species are already established.

Changes in invertebrate populations are also linked to changes in the substrate (Cummins and Lauf, 1969; Aggus, 1971; McLachlan and McLachlan, 1976). Newly flooded vegetation becomes covered with microflora, including bacteria, fungi and algae which provide a food resource and shelter for a number of species. The highest numbers of invertebrates have frequently been found in areas of recently flooded vegetation (Joffe, 1961; Paterson and Fernando, 1969; Aggus, 1971; Jones and Selgeby, 1974). For example, Glyptotendipes spp. and Endochironomus nigricans were abundant on flooded vegetation in Beaver reservoir, Canada, and are well adapted to these conditions (Aggus, 1971). As siltation increased Polypedilum digitifer and Tanytarsus spp. increased whilst Glyptotendipes spp. decreased.

The rate of decomposition of flooded terrestrial vegetation depends on water temperature and quality, as well as the vegetation type. In acid highland streams decomposition tends to be a slow process because of low temperature, low pH and high concentrations of phenolic compounds. In consequence, Campbell (1963) found plant remains in small highland reservoirs fifty years after submergence due to inhibition of decomposition. Hunt (1970) found that flooded vegetation in Llyn Celyn, north Wales, had not decomposed after three years. At Cow Green, a peaty upland reservoir in England, heather shoots were still undecomposed after five years (Armitage, 1977). After the decomposition of allochthonous organic material these reservoirs became more dependent upon organic matter brought in by the rivers, shore-line erosion material and autochthonous production (McLachlan, 1977).

The time taken to reach the peak invertebrate densities and biomass depends on climate, reservoir morphometry and surrounding topography. Ozhegova (1962) working on the Kairak-Kumsk reservoir, situated in a hot continental climate (Russia) recorded the highest biomass in the first year after filling.

In contrast, it takes longer for peaks to be reached in waters in temperate zones. For example, in Cow Green reservoir the numbers and biomass of organisms reached their peak three years after filling (Armitage, 1977). A peak in biomass in the second and fourth years after filling was found in two mountain reservoirs by Nursall (1952) and Jankovic (1972) respectively. Krzyzaneck (1970) recorded peak densities of chironomids in the third and again in the sixth year of the Gocalkowice reservoir, Russia.

Stage 4

The peak in densities and biomass is followed by a decline and eventually an equilibrium position is reached (Morduchai-Boltovskoi, 1961). Continuous succession of species in tropical reservoirs may reduce the time taken to reach a stable state. There is a possibility that Lake Kariba may have entered this final stage after a period of fifteen years (McLachlan, 1974). Temperate reservoirs may take longer to reach this stage due to seasonal declines imposed by winter conditions. Rzoska (1966) indicates that major changes in Russian reservoirs appear to be over after twenty-three years.

b) Ecology of the Chironomidae in lakes and reservoirs

Larvae of the Chironomidae are frequently the predominant macroinvertebrates in the sediments of water supply reservoirs and lakes. They occur in large numbers and play a major role in the ecology of the system. Pupae, although representing a short phase of the life cycle, may contribute significantly to the diet of fish. This is of particular importance in reservoirs that are managed as fisheries. Dense swarms of adult males may become a nuisance especially if they develop in urban areas.

(i) Distribution

Benthic organisms may be distributed in response to many factors especially those varying with water depth.

Welch (1935) demonstrated that the number of taxa declines with increasing depth. Brundin (1951) thought that oxygen concentration in the sediment was the most important environmental factor limiting the distribution of species. The distribution of chironomids in two shallow reservoirs with uniformly sloping sides was investigated by Mundie (1957). He suggested that factors such as different intensities of predation and depth of substrate were more important than oxygen concentration in limiting distributions. Thin sediment layers are thought to limit the distribution of Chironomus plumosus in some situations (Mundie, 1957; McLachlan and Cantrell, 1976). Wene (1940) found that sediment texture and organic content limited the distribution of larval chironomids. Substrate type has also been found to affect the rate of migration and settlement of Nilodorum brevibucca Freeman larvae in Lake Kariba (McLachlan, 1969).

Little experimental work has been undertaken to elucidate the factors influencing the movement, substrate selection and dispersal patterns of chironomid larvae in lakes and reservoirs. Cantrell and McLachlan (1977) investigated possible competition between Tanytarsus gregarius Kieffer and C. plumosus and their eventual distribution patterns. The activity of C. plumosus larvae apparently resulted in T. gregarius vacating their tubes. The displaced larvae then moved to the lake margin by positive phototaxis. C. plumosus larvae were prevented from colonizing the shallow water areas due to thin sediment layers. The size of larvae, however, rather than species, was shown to be critical in determining the outcome of competition for space.

Substrate selection has been observed in a number of species of chironomid larvae. Edgar and Meadows (1968) observed that Chironomus riparius Meigen larvae were unable to build tubes on sand and when presented with this substrate periods of active swimming were alternated with periods of resting on the substrate. The spatial dispersion of this

species was also investigated by Edgar and Meadows. When natural populations in a stoneware sink were aggregated by stirring they redistributed themselves in a regular pattern within forty-eight hours. This was repeated experimentally in the laboratory. However, Paterson and Fernando (1971) found the dispersion pattern of two species of chironomid larvae was related to the initial population density. When Chironomus abortivus Malloch and Glyptotendipes baripes (Staeger) were placed on uniform substrate they were found to be contagiously distributed at low population densities and randomly distributed at high population densities.

Davies (1973) has reviewed the complex effects of oviposition, larval migration and water currents in determining the distribution of chironomids in lakes.

(ii) Life histories and emergence

Seasonal changes in the number of chironomids emerging from lakes and reservoirs have been recorded by many workers (for example Humphries, 1938; Miller, 1941; Mundie, 1957; Morgan and Waddell, 1961; Sandberg, 1969). Surface and submerged emergence traps are frequently used to provide such data and an account of these traps is given by Edmonson and Winberg (1971).

Mundie (1957) used submerged emergence traps to investigate the ecology of chironomids in two reservoirs in south England. Many species, for example Procladius choreus (Meigen), Psectrocladius limbatellus (Holmgren), Endochironomus albipennis (Meigen) and Tanytarsus holochloris Edwards, were found to be bivoltine. The majority of species studied by Potter and Learner (1974) in a eutrophic reservoir in south Wales were also found to be bivoltine. Chironomus plumosus has been found to be bivoltine in shallow water and univoltine in deeper water (Johnson and Munger, 1930; Borutzky, 1939). Cricotopus sylvestris Fabricus, Polypedilum nubeculosum (Meigen) and

Tanytarsus lugens Kieffer are examples of species with more than two generations a year in the reservoirs studied by Mundie (1957). Chironomid species phenology appears to be determined by a variety of environmental factors and not simply by temperature. Anaerobic conditions, for example, may influence the fauna present and modify phenologies (Mundie, op. cit.).

Diel periodicity of pupal emergence has been investigated by several workers including Palmen (1955), Mundie (1959), Morgan and Waddell (1961) and Potter and Learner (1974). Generally the Tanypodinae and the Orthocladinae emerge during the day whilst the Chironominae are crepuscular and have a peak emergence at dusk or shortly after (Potter and Learner, 1974).

(iii) Production

The management of lakes and reservoirs depends on a knowledge of the processes occurring within the system. Production studies on benthic macroinvertebrates contribute to this information and may be particularly relevant where the system is managed as a fishery. Until the formation of the Productivity of Freshwater section of the International Biological Program relatively few studies on secondary productivity of English lakes and reservoirs had been carried out. The contribution by the United Kingdom to that section of the program has been reviewed by LeCren (1976). The methods and processes of production for all aquatic ecosystems has been reviewed by Mann (1969) and the secondary production in inland waters has been reviewed by Waters (1977).

As part of the International Biological Program in England the rate of production of four species of Chironominae and five species of Tanypodinae were calculated for Loch Leven, a shallow eutrophic lake in Scotland (Charles, East, Brown, Gray and Murray, 1974a; Charles et al., 1974b; Maitland and Hudspith, 1974; Charles and Murray, 1975). Estimates for the

sandy areas ranged from $150-420 \text{ kg ha}^{-1} \text{ yr}^{-1}$ and for the mud areas $335 \text{ kg ha}^{-1} \text{ yr}^{-1}$. These figures are similar to a value of $210 \text{ kg ha}^{-1} \text{ yr}^{-1}$ calculated by Potter and Learner (1974) for the Chironomidae in Eglwys Nunydd, a shallow eutrophic reservoir in Wales. Chironomid production accounted for 53% of the total production in this reservoir.

Turnover ratios or production to biomass ratios have been calculated for Chironomidae in a number of lakes and reservoirs (Miller, 1941; Kajak and Ryback, 1966; Sokolova, 1968; Johnson and Brinkhurst, 1971). Values range from 2 to 18.5 depending on the nutrient status of the water. The use of the production to emergence ratio, proposed by Spier and Anderson (1974), has been calculated by Jonasson (1972), Potter and Learner (1974), McCauley (1976) and Titmus and Badcock (1980). The production to emergence ratio accounts for the fate of elaborated tissue, which in the case of insect emergence may result in a net export from the system. Although calculations of this ratio have given wide ranges due to errors in sampling, it would appear that an appreciable proportion of the elaborated tissue is exported from the system.

(v) Chironomidae in the diet of trout

A general account of the diet of trout is given by Frost and Brown (1967). Trout are essentially carnivorous, eating mainly aquatic organisms but also taking terrestrial organisms when available. Ball (1961) suggests that trout feed on the accessible animals and exercise little or no selection. This is supported by Pentlow (1932), Neill (1938), Nilsson (1955), Graham and Jones (1962) and Siddiqui (1969). Hunt (1970) demonstrated that size, habits and mobility of the food organisms are more important than number in determining their presence in trout diets.

A number of workers have commented on the seasonal changes in the diet of trout. Allen (1938) recognised three seasonal phases in the diet of brown trout (Salmo trutta) in Lake

Windermere. The permanent bottom fauna were eaten from October to February, temporary bottom fauna from March to July and terrestrial insects from May to September. In contrast, Wilson^{et al.} (1975) could only distinguish two distinctive periods at Blagdon reservoir. Chironomid pupae were the main food item in summer and sticklebacks (Gasterosteus aculeatus L.) and Corixidae in the autumn. At Llyn Alaw brown trout were found to feed on bottom living organisms from September to May and on weed or mid-water animals from June to August (Hunt, 1970).

Few workers have attempted identification of chironomid larvae and pupae beyond family level in fish stomachs. Fish generally consume more pupae than larvae during periods of emergence. For example, chironomid pupae formed 20% by number of the organisms in 253 brown trout stomachs from Llyn Tegid whilst larvae formed only 0.2% (Ball, 1961). Pedley and Jones (1978) found that 24% of the total organisms in 378 brown trout stomachs were chironomid pupae whilst only 3% were chironomid larvae. In contrast to these findings, Hunt (1970) and Siddiqui (1969) found larger numbers of chironomid larvae than pupae in trout stomachs. In Llyn Alaw, Hunt (1970) found 1.4% of the organisms in brown trout stomachs were chironomid larvae. No pupae were found and only a few adults had been eaten. In Llyn Celyn 26.2% of the total stomach contents consisted of chironomid larvae and 35.4% pupae (Siddiqui, 1969). Adult chironomids appear to be rarely taken by trout in lakes and reservoirs. Holmes (1960) observed brown trout rising to Chironomus pupae in the evening but adults resting on the surface were not taken. In Lough Atorich, an Irish acid lake, winged insects were the chief component of the diet of trout, whilst in Lough Derg, an alkaline lake, they were only of minor importance (Southern, 1935). This may be related to the paucity of bottom fauna in acid pools and lakes (Robins, 1967; Hunt, 1970).

Pedley and Jones (1978) recorded twelve genera of chironomid larvae in brown trout stomachs from Llyn Dwythwch: Anatopynia, Pentaneura, Procladius, Orthocladius, Psectrocladius, Corynoneura, Metriocnemus, Pagastiella, Diamesa, Glyptotendipes, Microtendipes and Paratanytarsus. However, although four genera, Endochironomus, Polypedilum, Calopsectra and Heterotanytarsus, were found regularly and abundantly in the benthos they were not found in trout stomachs. In Llyn Alaw Hunt (1970) did not record Microtendipes diffinis (Edwards) larvae in trout stomachs although it was the most abundant species in the reservoir.

The proportion of chironomid larvae in the diet of trout does not appear to change with fish size (Hunt, 1970; Pedley and Jones, 1978). However, pupae and adults were found to be more abundant in the food of trout in the 300-430 mm size range than in smaller or larger fish (Hunt, 1970). Oliver (1968) showed that two year old fish in the 300-380 mm range at Eye Brook reservoir fed on nymphs and flies whilst older fish fed on bottom fauna and fish.

Hayne and Ball (1956) found that in the presence of fish the standing crop of the benthos remained more or less constant during a season. The production of benthic fish food during the same period was, however, estimated to be 17 times the level of the standing crop. When fish were removed the standing crop of the benthos increased to more than twice the original level but the benthic production rate declined to zero.

CHAPTER 2

THE STUDY AREA

Description of the Area

a) Location and general description

The reservoir known as Rutland Water ($52^{\circ}40'N$, $0^{\circ}37'W$), formerly Empingham Reservoir, lies midway between the towns of Leicester and Peterborough in the old county of Rutland (Fig. 1). The dam lies at the eastern end of the reservoir west of the town of Empingham and was built in the valley confluence of the northern and southern tributaries of the River Gwash. Hambelton peninsula divides the reservoir into two arms, running east-west down the river valleys, which join to form a deep central basin behind the dam (Plate 1). The reservoir lies in a rural area with rich arable and grazing farmland. The mosaic of fields before flooding is shown in Plate 2.

Picnic areas and car parks have been provided around the reservoir. These sites were carefully chosen to provide scenic views but also to keep their visual impact to a minimum. Sailing facilities are also provided on the reservoir for both casual sailors and for club members. The reservoir is stocked with brown trout and rainbow trout, many of which have been reared from the Water Authority's hatchery at Horn Mill. Fly fishing is allowed over most of the reservoir with certain zones restricted to bank fishermen or boat fishermen. Rowing and powered boats are available for hire by the fishermen. A 350 hectare nature reserve is located at the western end of the reservoir and is expected to become a nationally important wildfowl refuge. A series of lagoons is located in the south arm of the reservoir, within the nature reserve area, providing an area of stable water level free from disturbance.

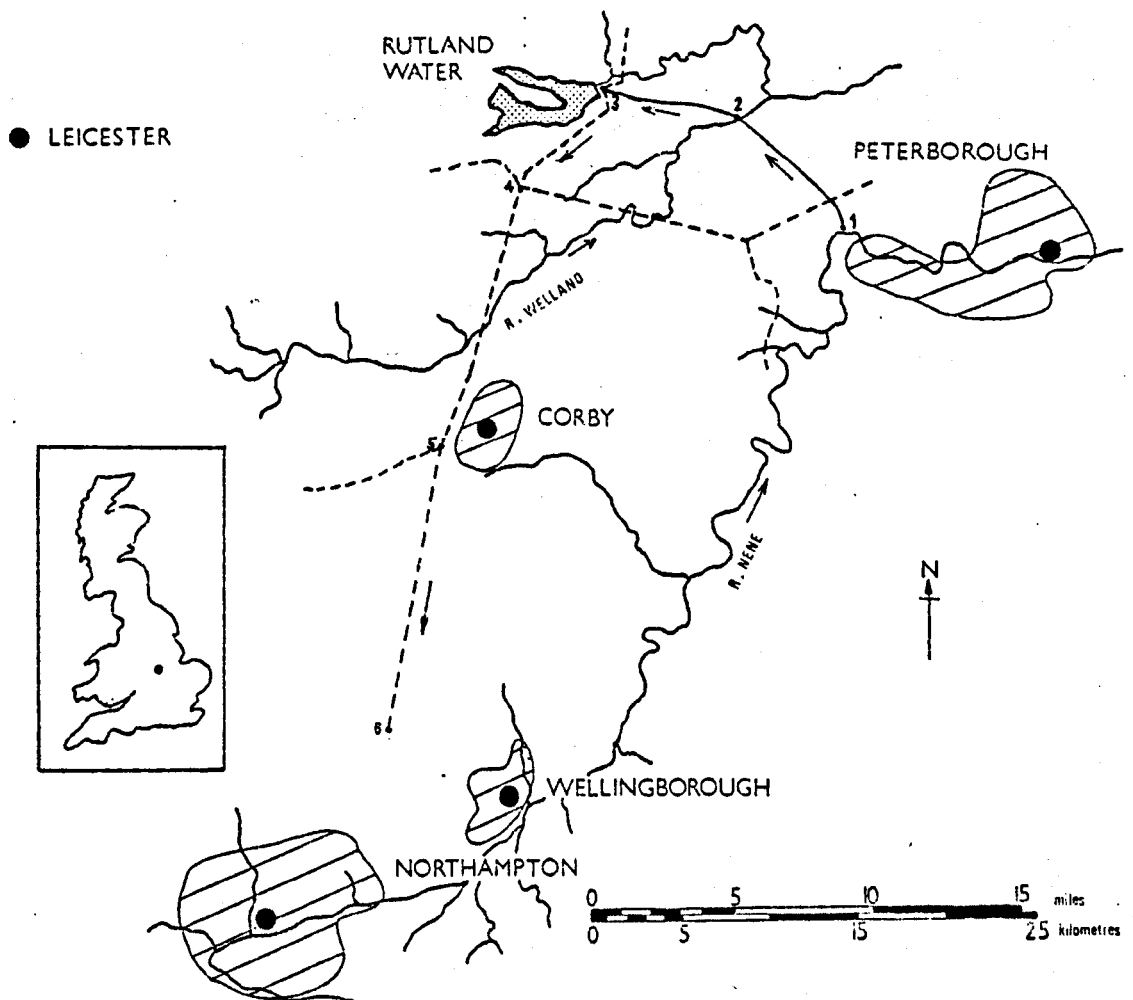


Fig. 1. Rutland Water pump storage scheme. (1) Wansford intake pumping station; (2) Tinwell intake pumping station; (3) Empingham pumping station; (4) Wing treatment works; (5) Beanford service reservoir; (6) Hannington service reservoir; — inlet aqueduct; ---- delivery pipeline.



Plate 1. Aerial view of Rutland Water looking west over the dam. Hambleton peninsular can be seen in the background and the trout holding tanks can be seen below the dam in the foreground.



Plate 2. Aerial view of the general area before flooding

b) Geology

The soil in the catchment area is derived from Jurassic clays and limestone. Along the stream bed of the River Gwash alluvial deposits and river gravels of Pleistocene and Recent origin occur (Fig. 2). Silt and marlstone deposits occur at the ends of the north and south arms of the reservoir.

Although geologically the area satisfied the design features, being fault free, watertight and supporting the weight of the dam, there has been some loss of water by seepage through old wells located on the valley floor.

c) Meteorology

Freshwater ecosystems, particularly large lakes and reservoirs, are influenced by meteorological conditions in a number of ways. Solar radiation is the major source of heat that is directly absorbed and raises the temperature of the water. Heat is lost by radiation from the surface and by evaporation and conduction. These in turn are affected by humidity and wind speed. Temperature may be a limiting factor in the distribution of some benthic invertebrates but it is probably of less importance directly than via physical effects it produces. Differential heating of water results in density changes and thermal stratification may occur. The resulting thermocline may influence oxygen content, water chemistry and water movement. All have major impacts on the fauna.

Wind produces both horizontal water currents and turbulence effects. Turbulence is important in the mixing of water and in heat transport and water chemistry. Oscillations of the whole lake, seiches, are usually produced by pressure differences across the surface. These may be caused either by wind or by localised heavy rain.

Little is known about the influence of large lakes and reservoirs upon the local climate.

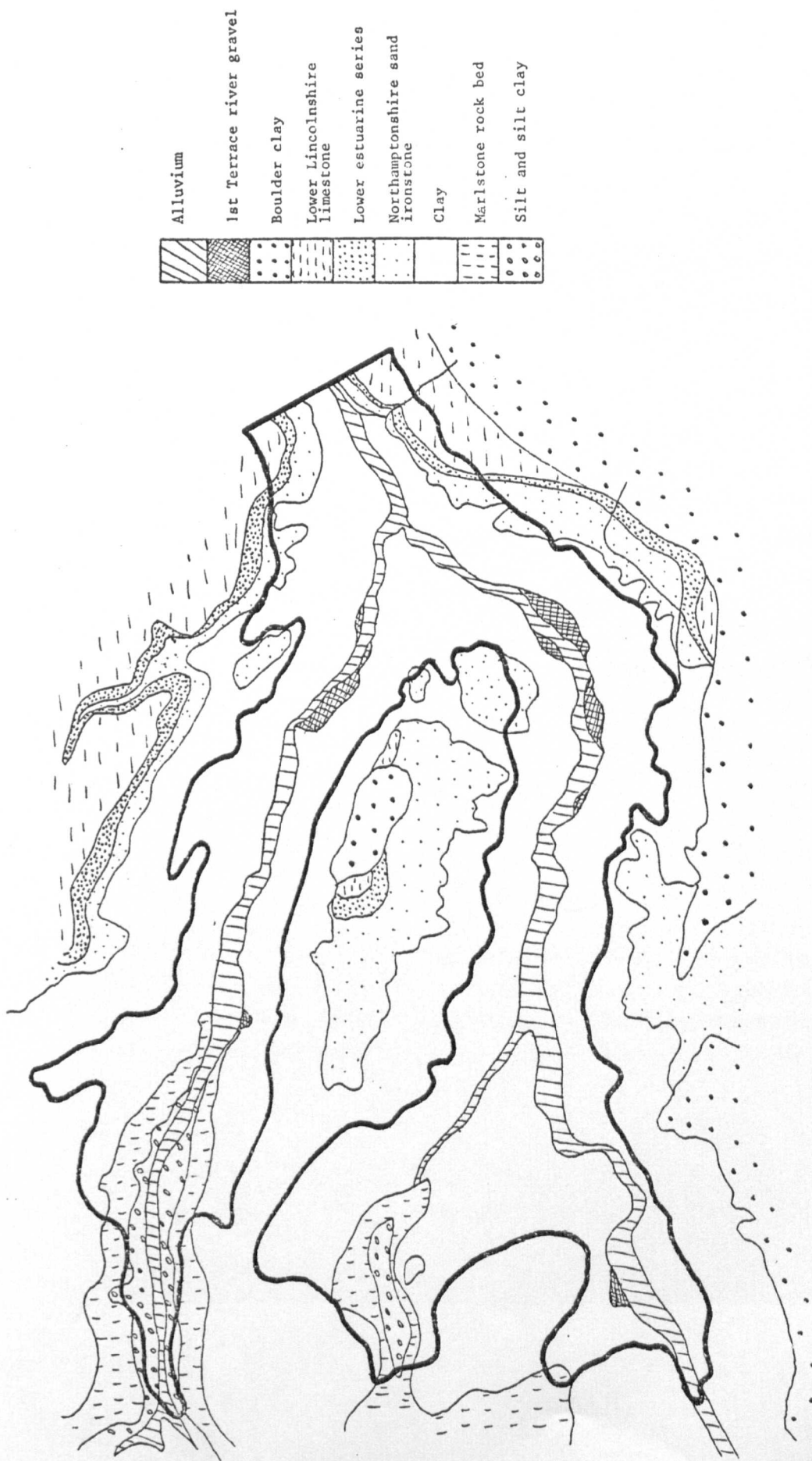


Fig. 2. Geology of the Rutland Water area

Meteorological data from 1975 to 1979 have been presented below as they are of direct relevance to the events that occurred in the reservoir during the study period.

Rutland Water is situated where the climate is temperate. Westerly and south-westerly winds from the Atlantic bring moist air which is relatively cool in summer and relatively warm in winter due to the influence of the Gulf Stream. The sun is potentially visible for 16 hours 38 minutes at the summer solstice (22nd June 1979) and for 7 hours 50 minutes at the winter solstice (22nd December 1979).

All meteorological data were recorded at the Royal Air Force station Wittering, located 8 km south-east of the reservoir.

The mean monthly air temperatures from January 1975 to April 1979 are shown in Figure 3. The winter temperatures for 1974/75 and 1975/76 were higher than the average given for the 1961-1970 decade. The summer temperatures were also above the decade mean. The highest mean monthly maximum temperature (25°C) for the whole period was recorded in July 1976. The seasonal values for 1977 and 1978 were similar to the decade means. During January and February 1979 the mean temperature remained below 1°C and for two days the reservoir was covered by ice.

The high summer temperatures during 1976 reflect the total hours of sunshine (Fig. 4). For example, in June 1976 there were 284 hours of sunshine compared to only 170 hours in June 1978.

The prevailing winds in the area of Rutland Water are south-westerly (Fig. 5). Easterly winds were stronger in 1976 than the other years. Wind speeds fluctuate both on an hourly and seasonal basis but the monthly means tend to be higher in the winter period (Fig. 6). The data for 1976 are atypical, the

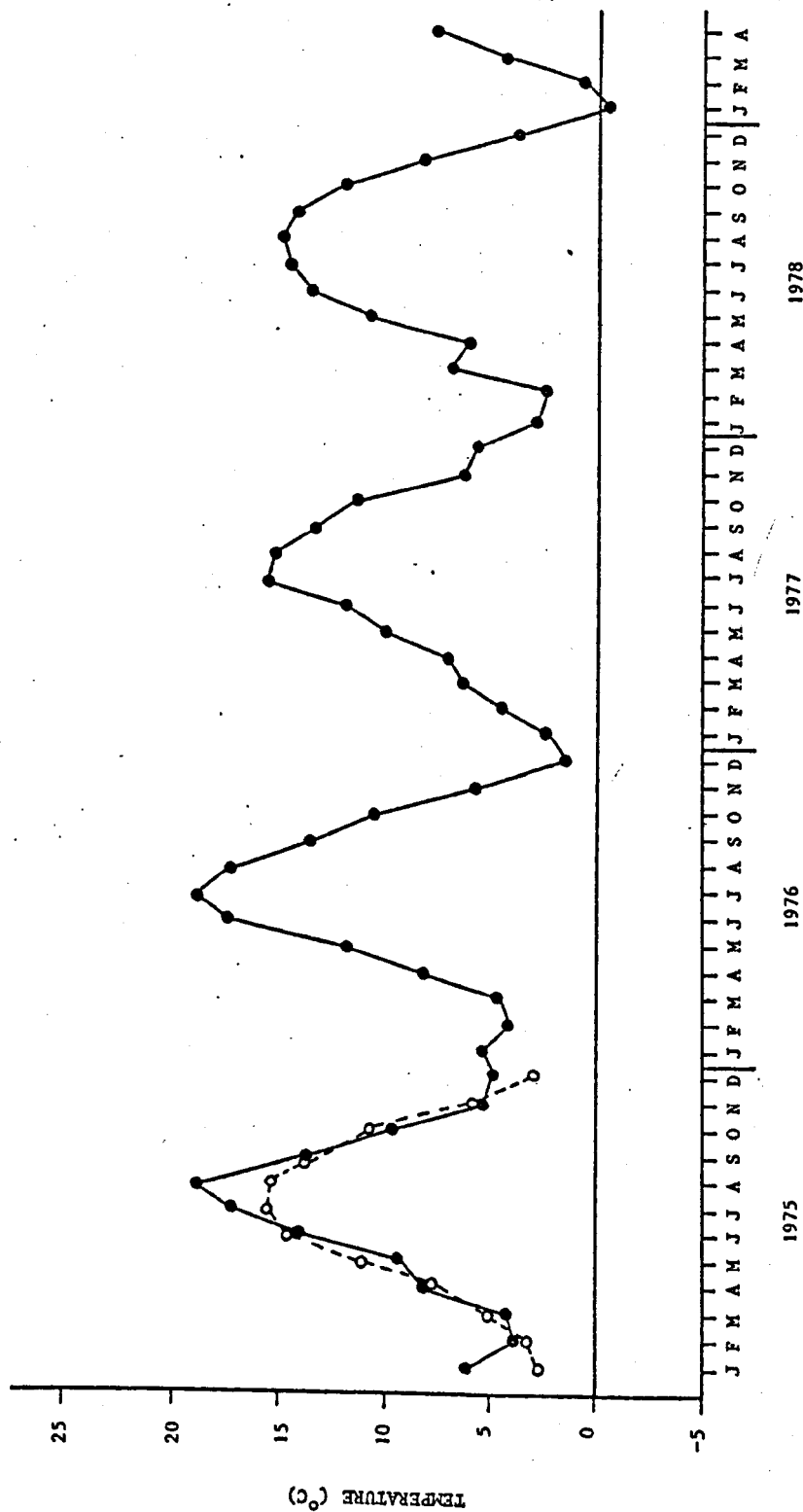


Fig. 3. Mean monthly air temperatures recorded at RAF Wittering. Means calculated from daily mean maximum and mean minimum temperatures. Open circles decade (1961-1970) means.

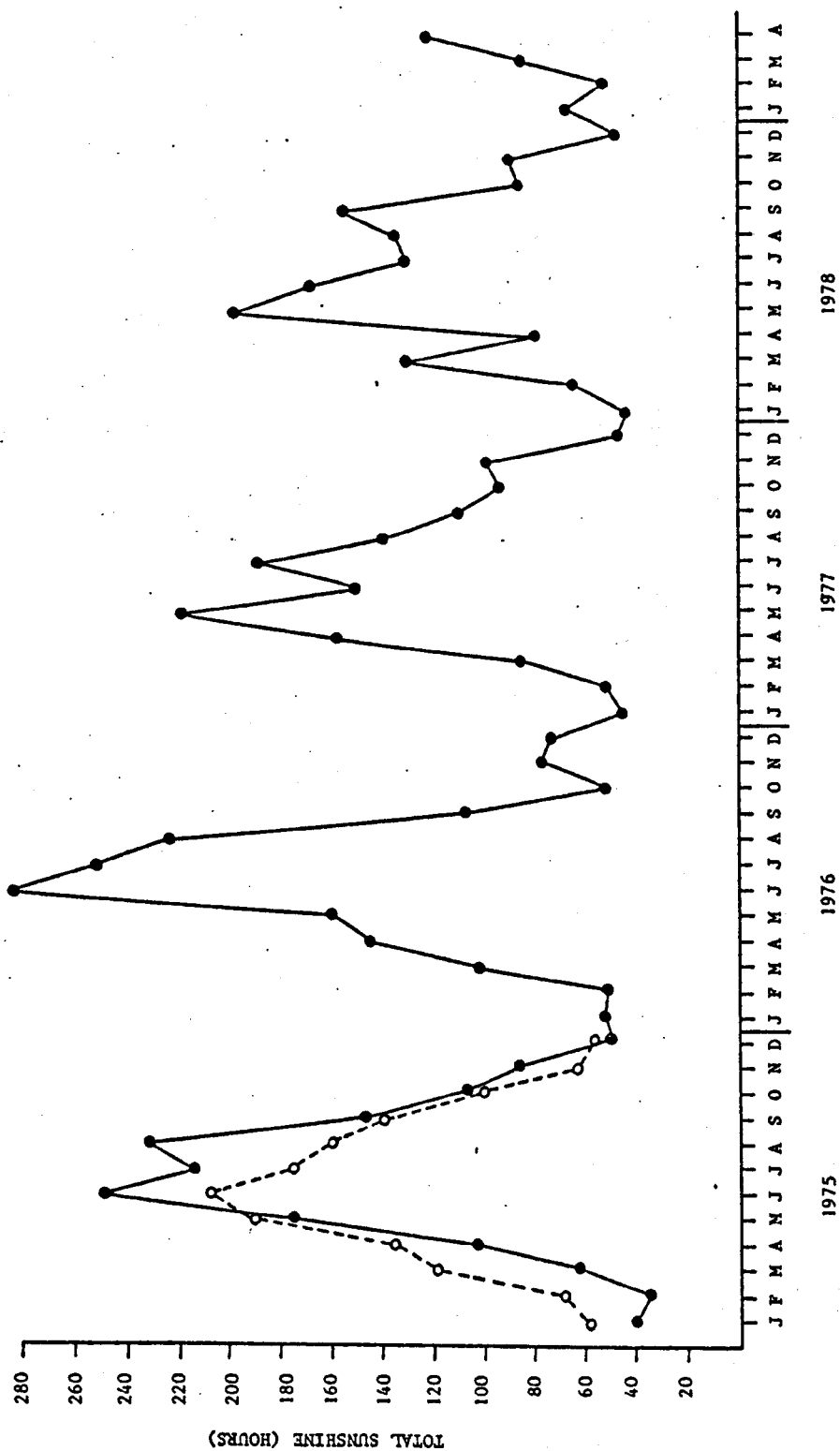


Fig. 4. Total number of hours of sunshine monthly recorded at RAF Wittering.

Open circles decade (1961-1970) means.

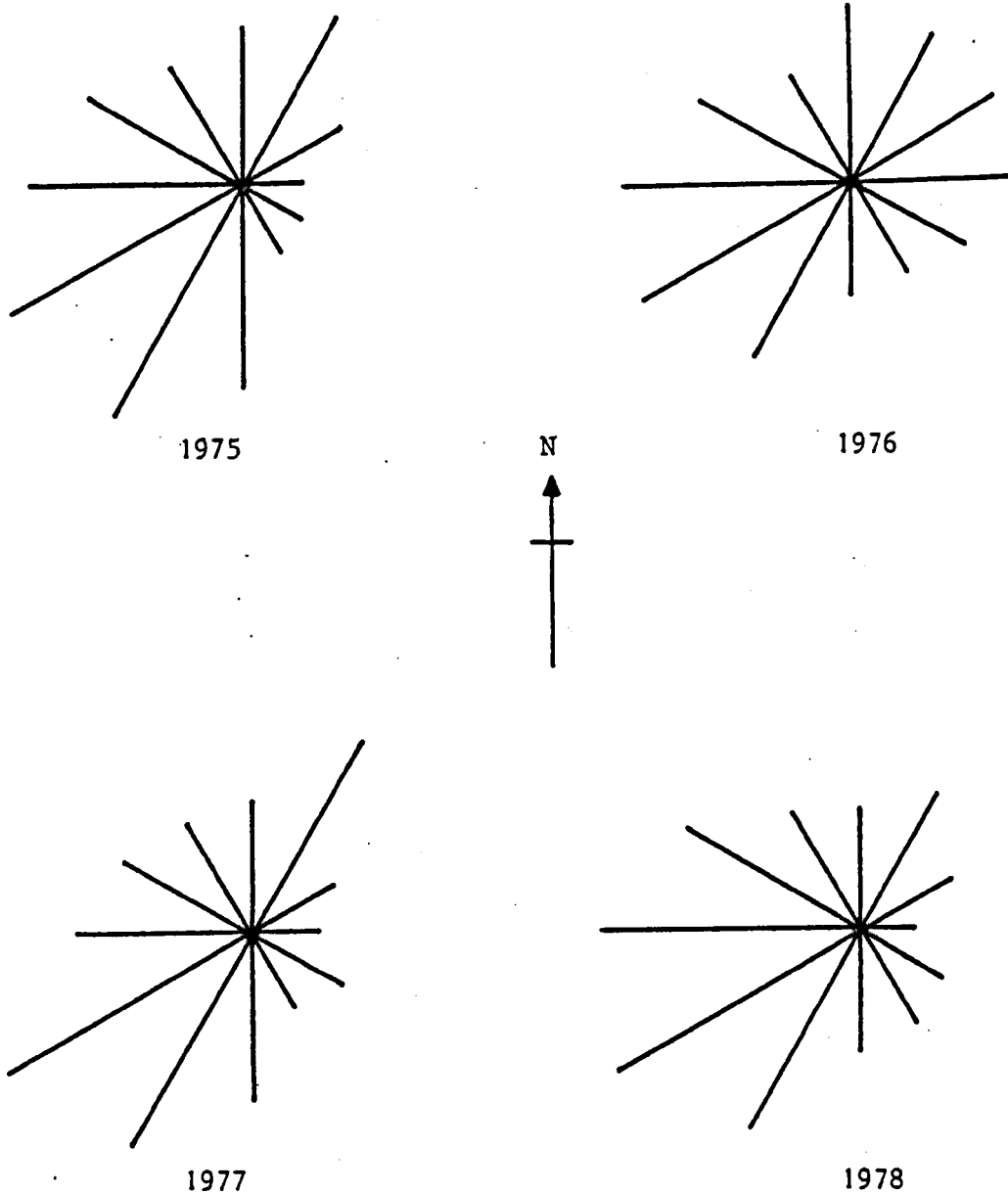


Fig. 5. Percentage frequency of wind direction annually from 1975 to 1978, calculated from hourly readings recorded at RAF Wittering.

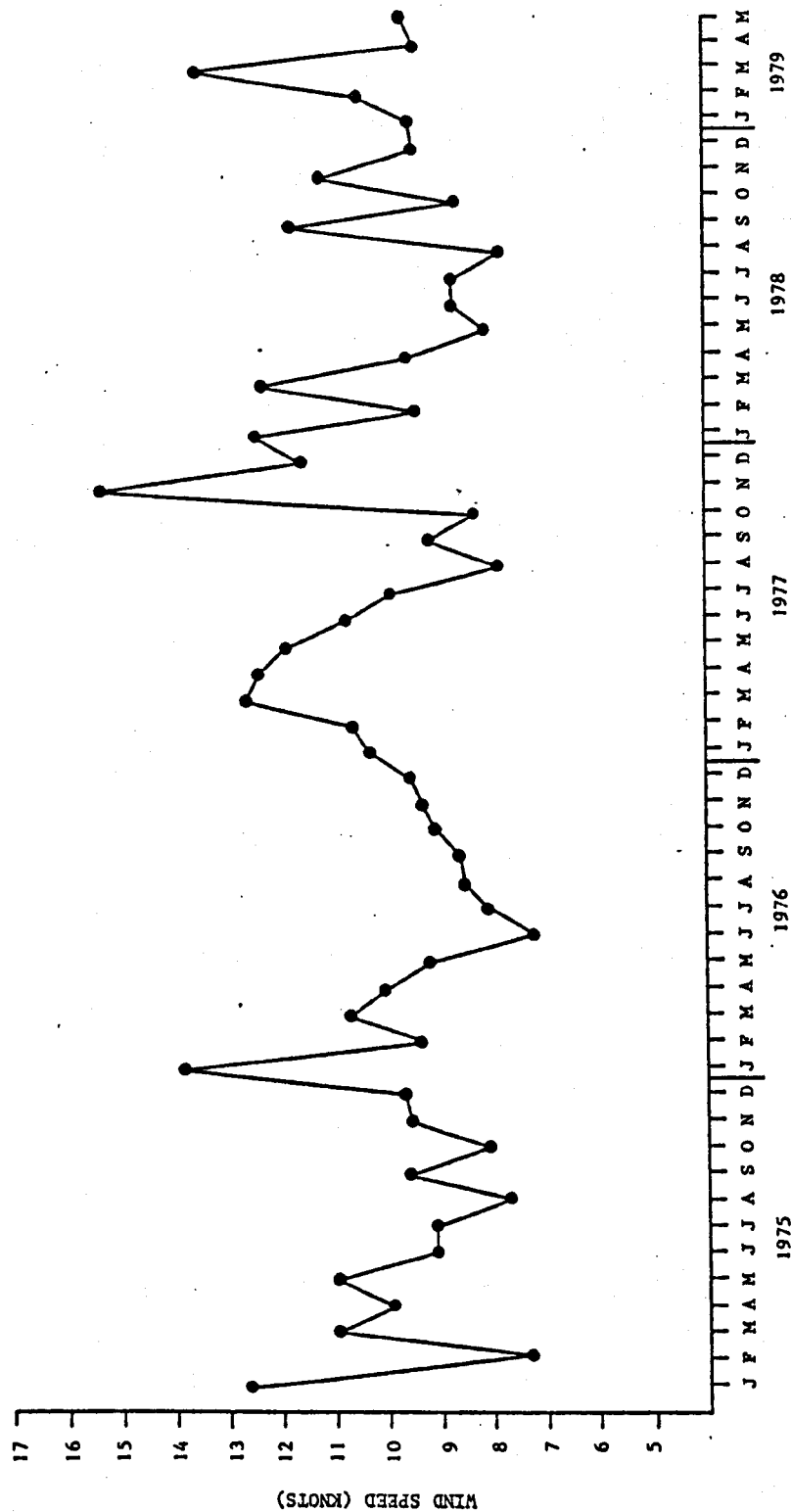


Fig. 6. Mean monthly winds speeds calculated from hourly readings recorded at RAF Wittering.

mean monthly wind speed increasing gradually from June to February 1977.

The mean monthly rainfall values tend to fluctuate a great deal (Fig. 7). There was an extensive period of low rainfall from October 1975 to July 1976, resulting in the "drought" conditions during 1976. Above average rainfall was recorded from August 1976 to January 1977, in August 1977 and December 1978.

A summary of the weather conditions for 1975 to 1978 is given in Table 1. 1975 and 1976 were above average in terms of sunshine and temperature and below average in terms of rainfall. 1977 and 1978 were below average in terms of sunshine and temperature and high in terms of rainfall.

Rutland Water

a) Pump storage scheme

Water for the reservoir is pumped from two rivers, the Welland and Nene, situated to the south-east of the reservoir (Fig. 1). The natural catchment provides a third source of water. The intakes for the Rivers Welland and Nene are situated at Wansford and Tinwell respectively (Fig. 1). After treatment the reservoir water is distributed to the Corby and Northampton areas. As these areas are upstream of the intake sites some recycling of water will occur.

b) Reservoir features

The reservoir when full covers an area of 1,260 hectares, has a volume of $124 \times 10^6 \text{ m}^3$ and a shoreline of 38.6 km. The average depth is 10.7 m with a maximum depth of 33.5 m in the central basin.

The design features of Rutland Water are based on the results of two theoretical studies undertaken by the Water

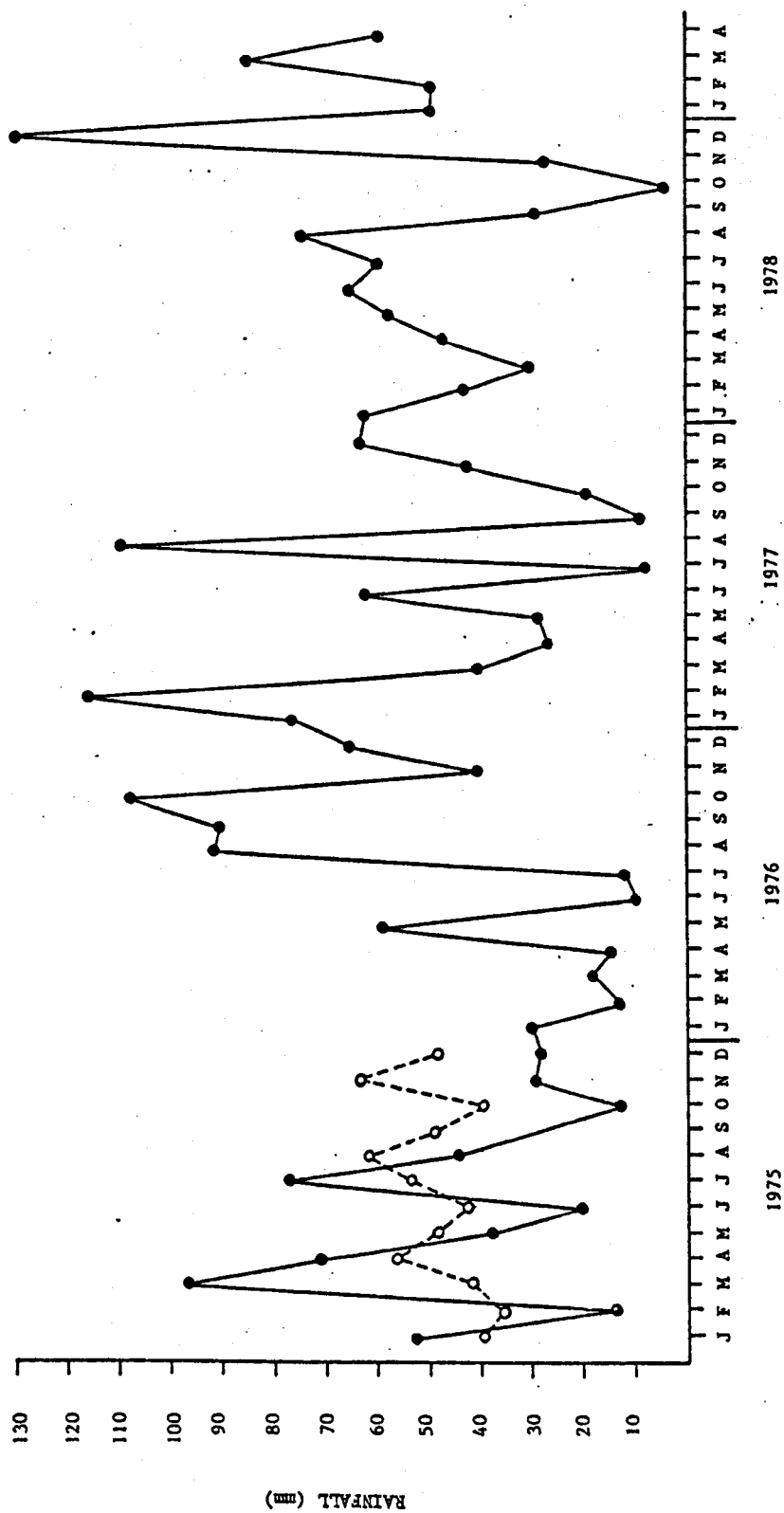


Fig. 7. Mean monthly rainfall calculated from daily readings recorded at RAF Wittering.
Open circles decade (1961-1970) mean.

Table 1: Summary of weather conditions for the four year study period. Values are calculated from monthly means.

	1975	1976	1977	1978	1961-70
Total sunshine (hrs)	126	132	117	112	123
Mean temperature (°C)	9.8	10.1	9.3	8.4	9.3
Rainfall (mm)	4.8	4.7	5.1	5.3	4.9
Wind speed (knots)	9.6	9.5	11.0	9.9	-

Research Association (1971) and the Anglian Water Authority (1972). The main design and topographical features of the reservoir are shown in Figure 8. The pumped river water enters through four jets directed westwards in the south arm. Two draw-off towers are located in the reservoir. The main tower is at the southern end of the dam and has four draw-off points at different depths. A secondary tower is situated in the north arm (Fig. 8) again with draw-off points at several depths. A limnological tower, located in the central basin of the reservoir, may be used to automatically record temperature and oxygen concentrations at 2 m intervals through the water column. Readings may be taken at fixed time intervals or continuously. A grid of twelve aerators are laid on the floor of the reservoir in the central basin and can be operated to break down stratification when necessary.

Prior studies carried out by the Anglian Water Authority indicated that, as the nutrient loadings for the incoming river water were high, eutrophic conditions could be expected. Effluent from the Oakham sewage tertiary treatment plant also enters the reservoir. The location and orientation of the inlet jets and the transfer of the sewage effluent input from the north arm to the south arm were designed to make the south arm the more nutrient rich. It was envisaged that algal growths would, thus, occur in this area and deplete the water of nutrients before it circulated into the north arm. The secondary draw-off tower was thus located in a zone of likely higher water quality whilst the main draw-off tower was located in a zone least likely to be affected by surface blown algal blooms carried by the prevailing south-westerly winds.

c) Filling regime

The reservoir began to fill in February 1975 and all impounded water during 1975 was derived from the natural catchment (Figs. 9 and 10). In January 1976 the pumps were

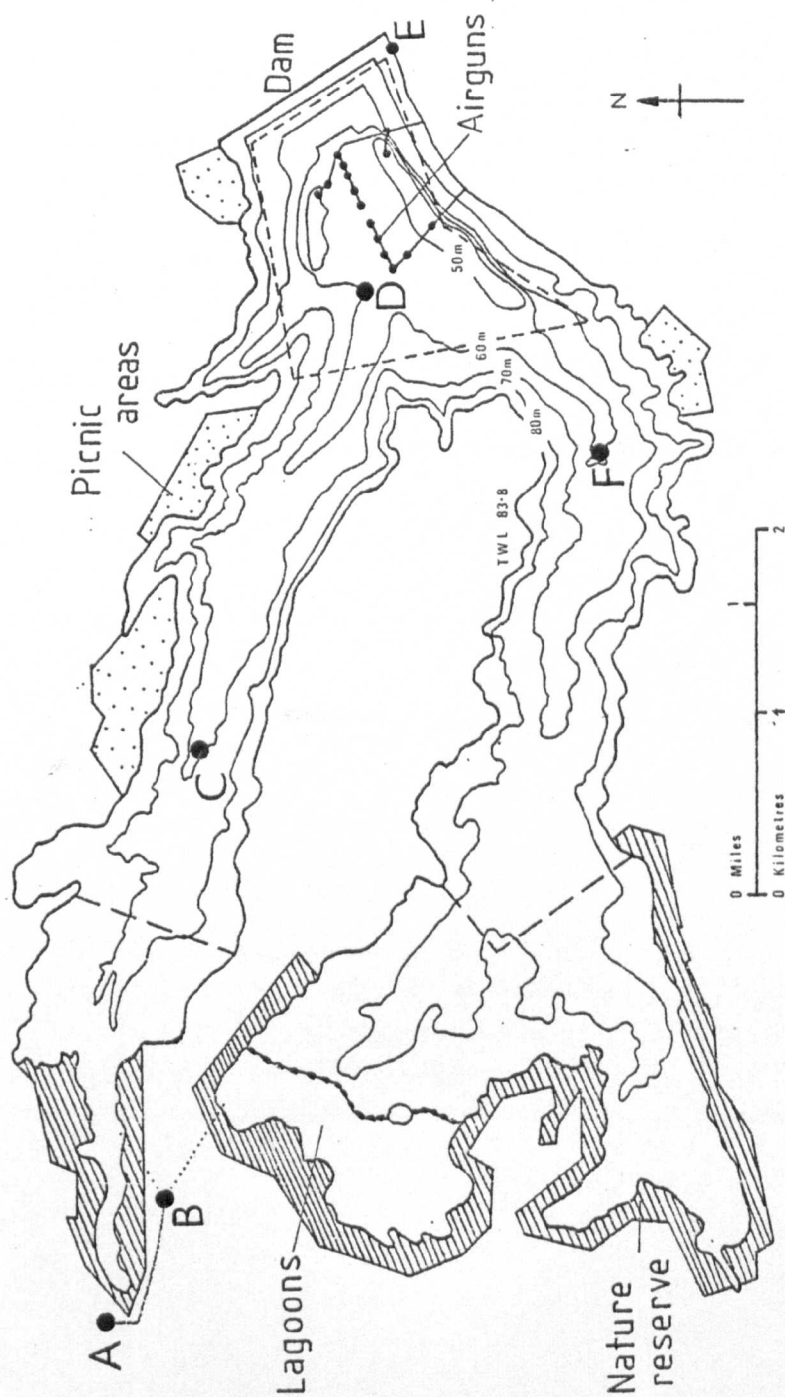


Fig. 8. Topographical features of Rutland Water. (A) Oakham sewage works; (B) Land treatment works; (C) Secondary draw-off tower; (D) Limnological tower; (E) Draw-off tower; (F) Inlet; --- Limit of sailing; Trolling area.

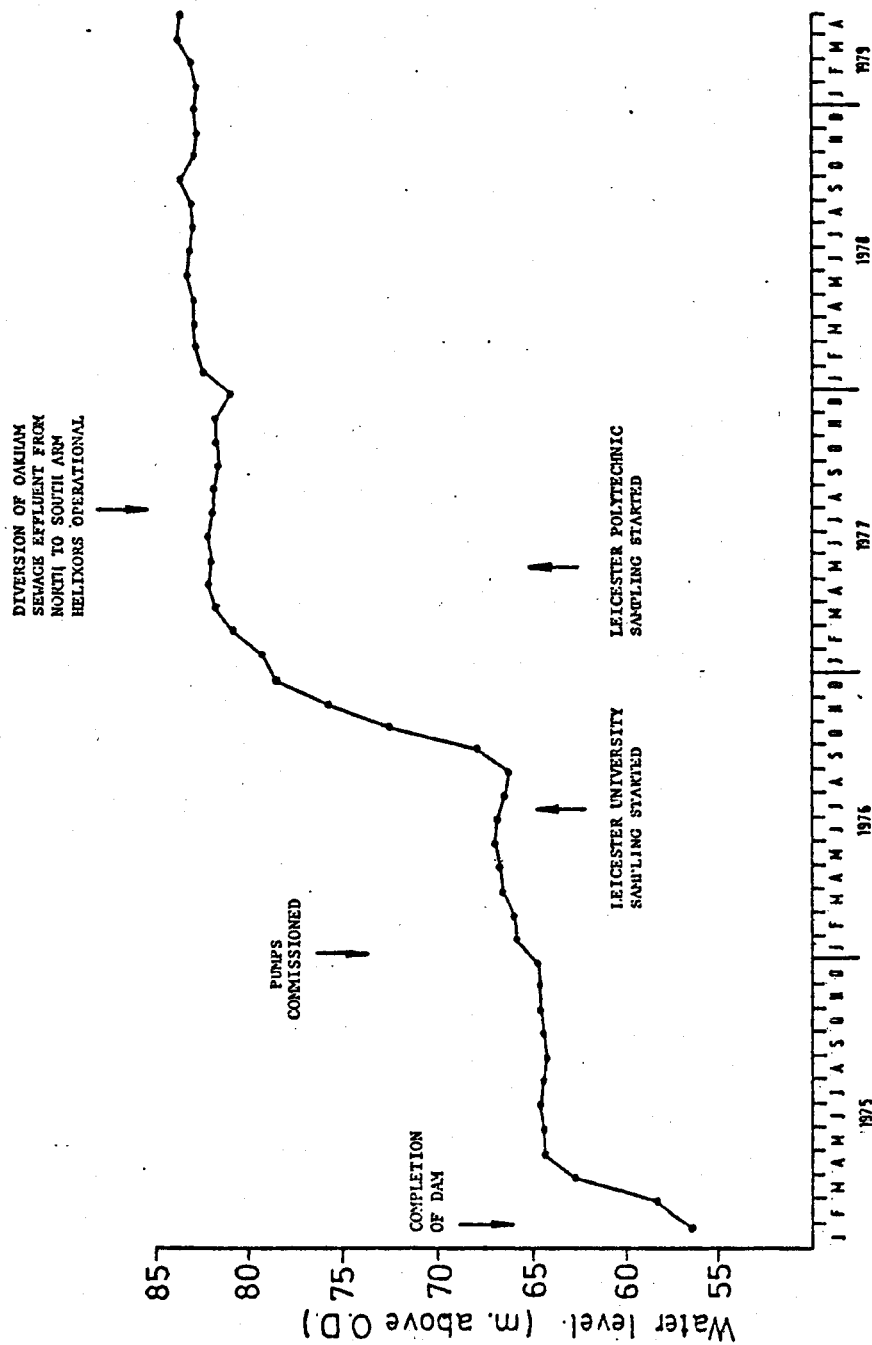


Fig. 9. Filling of Rutland Water

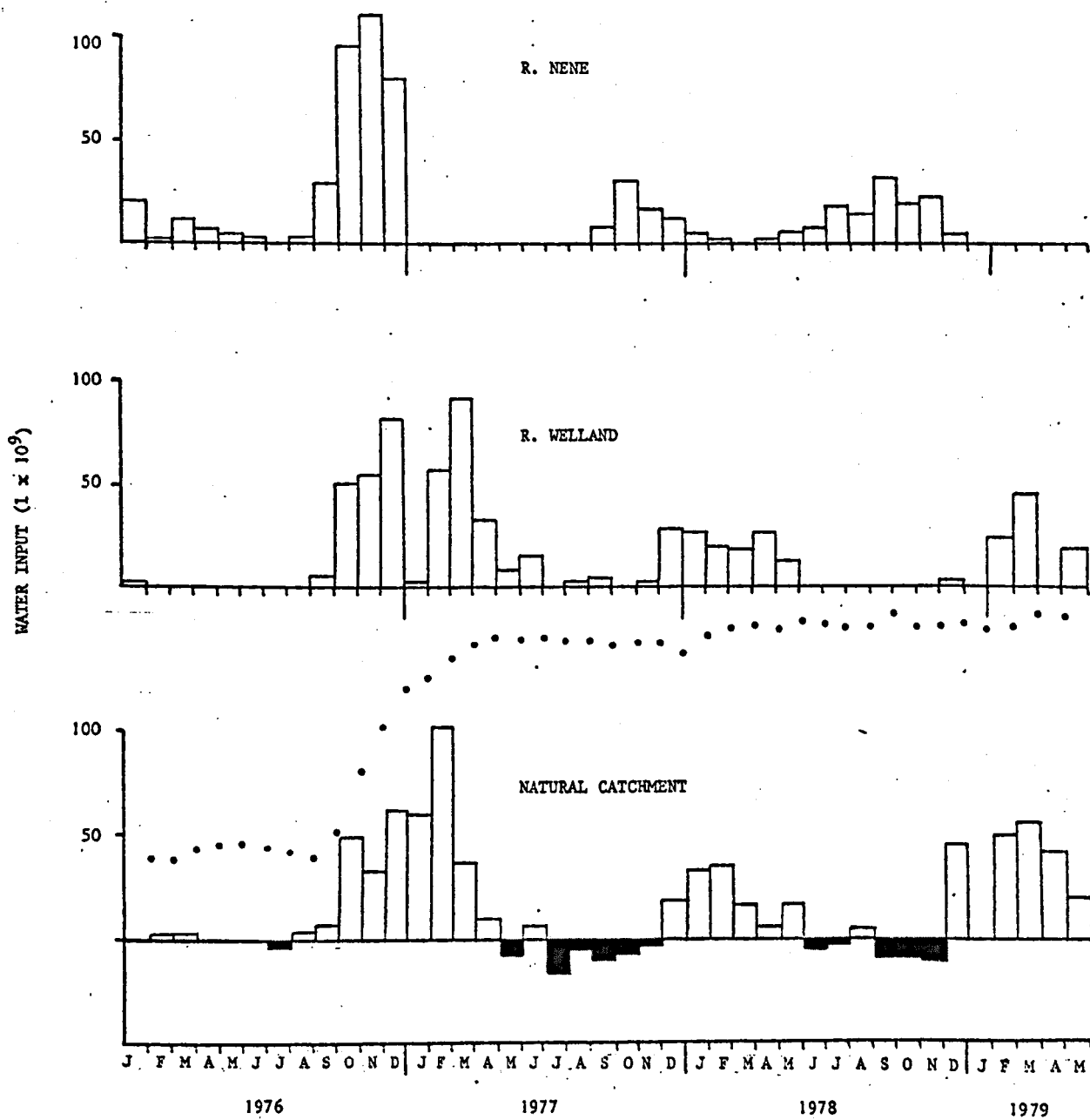


Fig. 10. Water balance for reservoir. Dots show increase in water level for the reservoir (see Fig. 9).

commissioned to supply water from the Rivers Nene and Welland. Throughout 1976 water was derived from all three sources. From the end of December 1976 to June 1977 no water was abstracted from the Nene because the concentration of sulphate initially, and later nitrate, exceeded the World Health Organisation's recommended limits. This followed the drought of 1976 and was attributed to excessive leaching from soils. Pumping also ceased from the River Welland during the first week of January 1977 because of high concentrations of nitrate.

Pumping during 1976 was intermittent due to the dry summer. From June to September 1976 the water level fell (Fig. 9). High rainfall occurred during the winter 1976/77 (Fig. 7) and the reservoir water level increased from 76 m O.D. to 82 m O.D. This corresponds to an increase in volume of 57×10^9 l and surface area of 4.6×10^6 m², in a period of under six months. Curves relating depth to capacity and surface area are shown in Figure 11. The proportion of water from the three sources was actually the reverse of the expected values. The River Nene, with the largest flow rate ($14.6 \text{ m}^3 \text{ s}^{-1}$ during 1974-75) only contributed 25% of the reservoir water, 38% was derived from the River Welland and 40% was derived from the natural catchment.

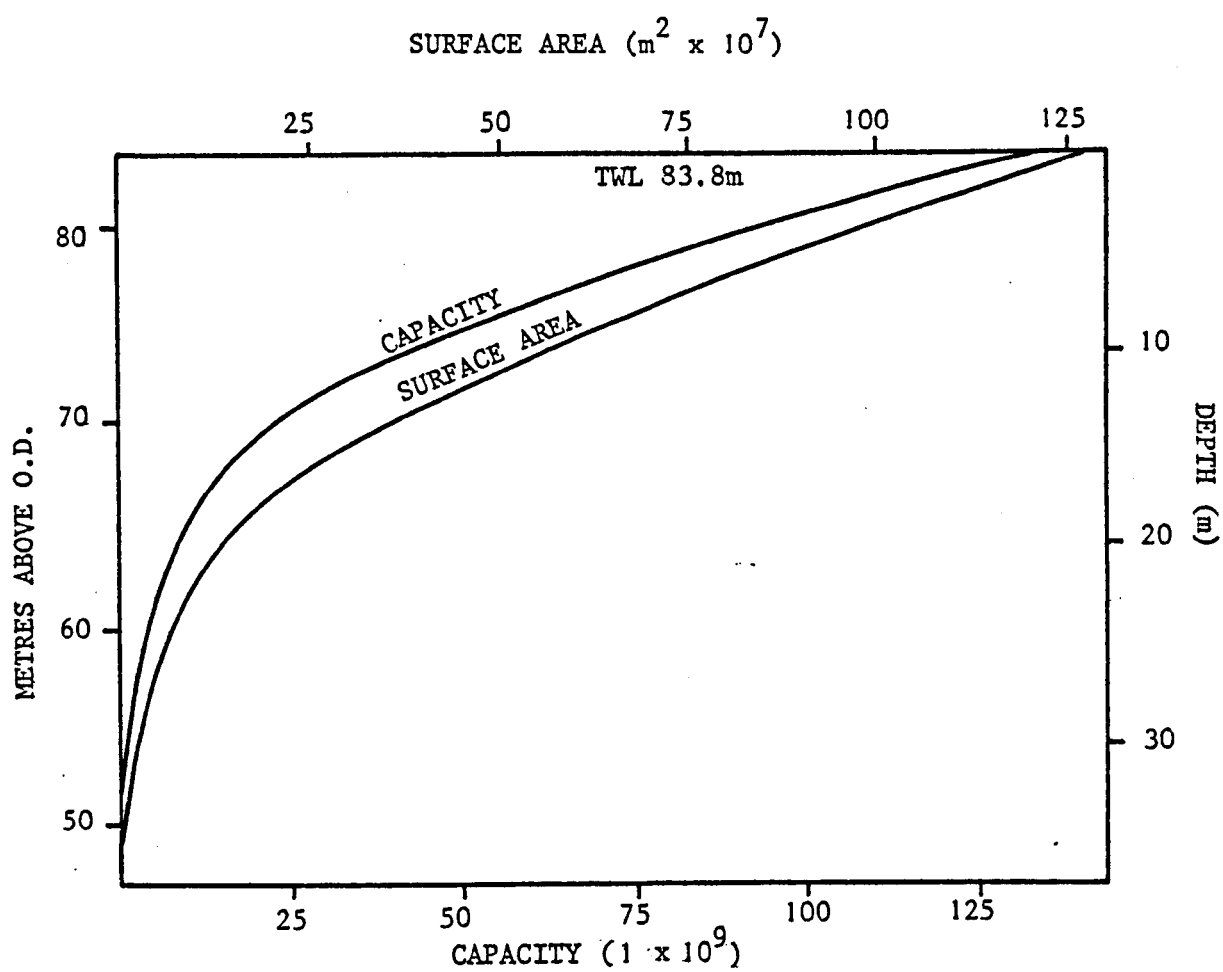


Fig. 11. Depth to capacity and surface area curves for Rutland Water.

CHAPTER 3

MATERIALS AND METHODS

Monitoring by Anglian Water Authority

a) Water Chemistry

Ten open water sites, the two draw-off points and the two sites of water abstraction from the rivers are routinely monitored for eighteen physico-chemical parameters. The locations of the reservoir sampling sites are shown in Figure 12. Water samples were collected using a Friedinger bottle at 0.5m depth on a weekly or fortnightly basis. Methods for the chemical analysis are described by Department of the Environment (1972). Nitrate-nitrogen and silica were measured by auto-analysis from 9.6.76. and 25.5.77. respectively.

Oxygen and temperature profiles are based on measurements taken at weekly intervals at the limnological tower. Surface (0.5m depth) temperature and oxygen measurements were also taken at the sites shown in Figure 12.

b) Phytoplankton

Phytoplankton populations were estimated from 5m Friedinger tube samples taken at weekly intervals from several of the sites shown in Figure 12. Chlorophyll-a was extracted with hot methanol and concentrations were calculated using the equation of Talling and Driver (1963).

Benthic Macroinvertebrate Sampling

a) Choice of sampling devices

Sampling methods may be divided into "passive methods", such as those that involve the use of natural and artificial substrates, and "active methods" that require the participation of an operator. These include methods involving scoops, grabs

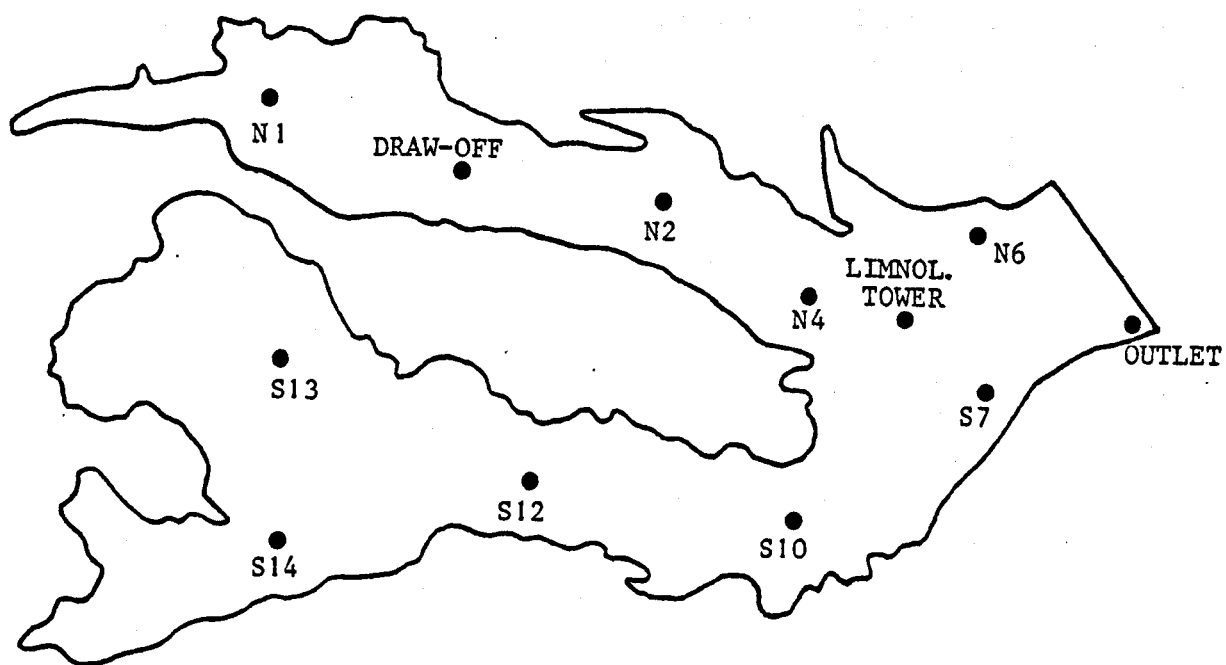


Fig. 12. Sampling sites for physical and chemical analysis

and corers. Reviews of "active" and "passive methods" may be found in Edmonson and Winberg (1971) and Hellowell (1978). Brinkhurst (1974) provides a review of active sampling devices, especially grabs. A comprehensive bibliography dealing with active sampling methods has been compiled by Elliott (1978).

The practicability of artificial substrate samplers is restricted due to the length of time required for colonization by invertebrates and the frequently unrepresentative fauna that they collect (Hellowell, 1978). Samplers that require marking with surface buoys are also prone to damage or loss, particularly on heavily used reservoirs such as Rutland Water. Quantitative active samplers may be reduced to three categories: diver operated suction and airlift samplers, coring devices and grab samplers. The most efficient, in terms of representative catches, are those operated by divers, but these methods require specialist equipment and expertise. Corers meet the requirements of most benthic invertebrate surveys as they sample a well defined area and disturb the surface sediment very little. However, many corers cannot penetrate hard substrates and were considered unsuitable in the reservoir because of the variety of substrates. Grab samplers are the traditional tools for sampling lakes and reservoirs and a wide variety is available. A modified van Veen grab, designed by Wilson, Bristol University, was chosen for the present study due to its ease of use, low construction costs, simple operating mechanism and efficient biting profile.

b) Modified van Veen grab

The original van Veen grab (Fig. 13a) has been compared with several marine samples: an Agassiz trawl (McIntyre, 1956), a Reineck boxcorer (Benkema, 1974) and a Forester anchor dredge (Gage, 1975). Thamdrup (1938), Ursin (1954), Birkett (1958), Kutty and Davies (1968) have all compared the van Veen grab with the Petersen grab. Generally the van Veen grab was found

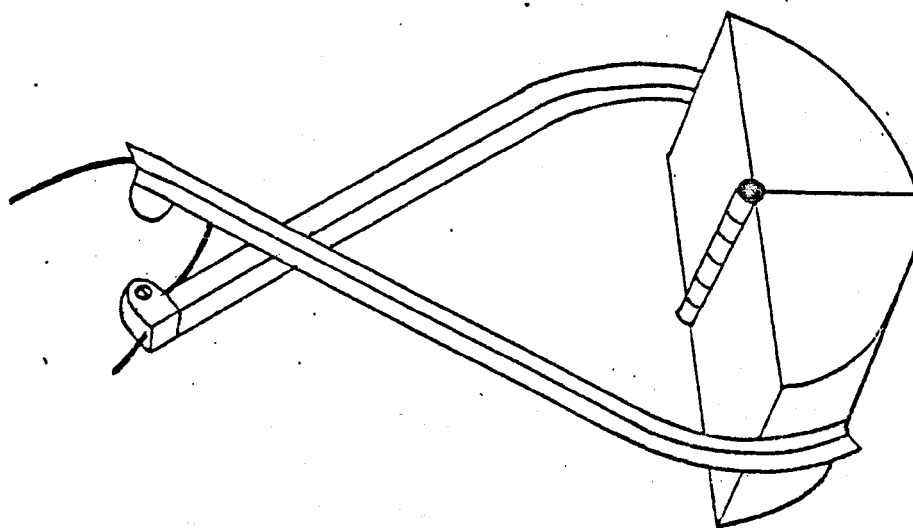


Fig. 13a Original van Veen grab.

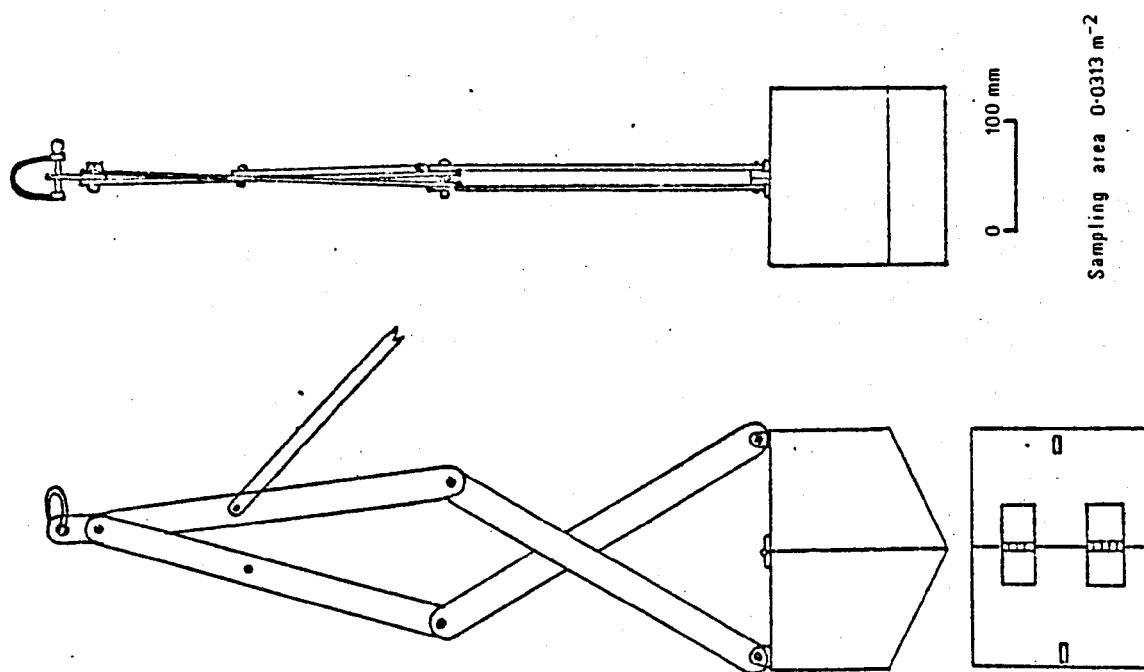


Fig. 13b Modified van Veen grab.

to have a better cutting profile and was more efficient. The cutting profiles of the Petersen, van Veen and Smith-McIntyre grabs in soft and hard sand were studied by Gallardo (1965). In these air-to-ground trials the most uniform depth penetration over the whole area sampled was achieved with the van Veen grab. Wigley (1967) compared the efficiencies of the van Veen and Smith-McIntyre grabs underwater using cine film. Ping-pong balls were used to indicate the effect of the shock wave as the grab descended. The van Veen grab produced the strongest shock wave. The lifting characteristics of the 0.1m^2 van Veen grab were investigated by Lie and Pamatmat (1965). Subaqua divers observed the grab underwater and reported the need to lift the grab carefully from the bottom. A jerk resulted in material being left behind. The observed horizontal approach of the jaws when closing confirmed the profile described by Gallardo (1965).

In the modified van Veen grab (Fig. 13b, Plate 3) the arm and chain closing mechanism is replaced by two scissor-like arms. The cross member that holds the grab open on descent is released automatically when the grab hits the bottom. The weight of the grab closes the jaws as it is lifted from the bottom.

c) Possible grab defects

Five possible defects in the operation of the modified van Veen grab are illustrated in Figure 14 and were investigated by sub-aqua diving.

1. Shock wave

The severity of the shock wave caused by a descending grab is directly related to the flow of water through the tops of the jaws (Wigley, 1967). This effect can be reduced, as in the original van Veen grab, by the insertion of a mesh screen or hinged flaps in the tops of the jaws to allow a flow of water through the grab as it descends.

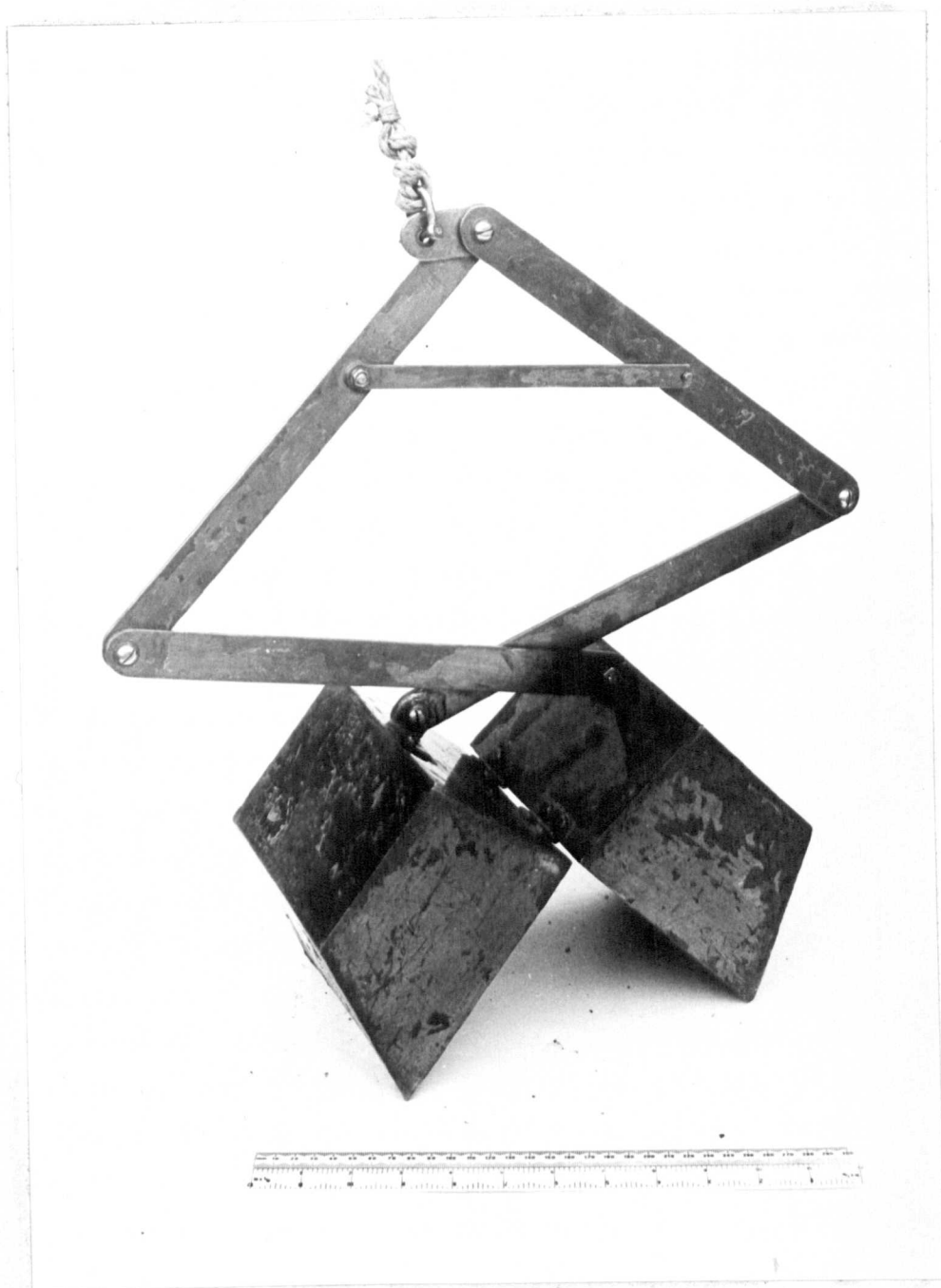
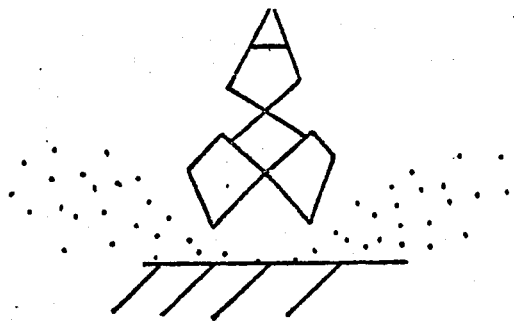
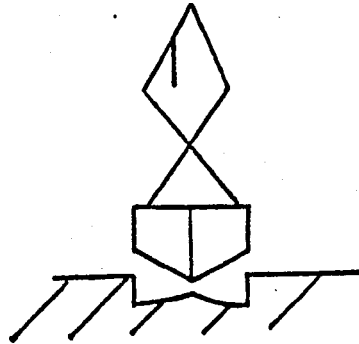


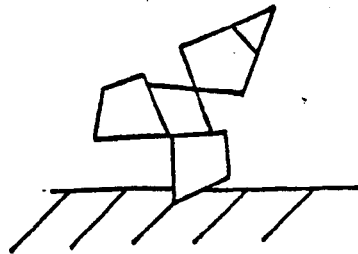
Plate 3. Modified van Veen grab



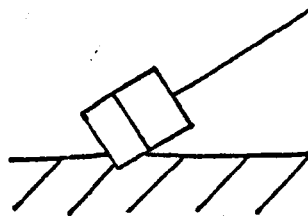
SHOCK WAVE



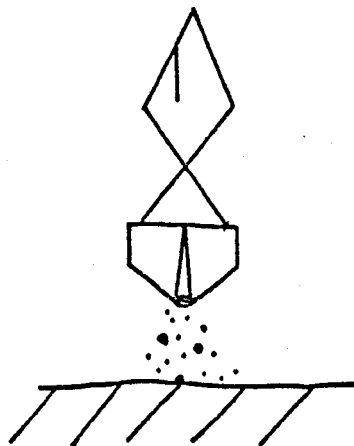
CUTTING PROFILE AND
PENETRATION



TILTING - SIDE ON



TILTING - END ON



LOSS OF MATERIAL ON HAUL

Fig. 14. Possible grab defects.

Observations of the grab underwater indicated that the shock wave effects could be considerable when the grab was dropped heavily into deep silty substrates (Plate 4). The substrate at Rutland Water, during the early stages of the investigation, consisted mainly of decaying terrestrial vegetation. Few silty areas were found and shock wave effects were not considered important. After accumulation of silty deposits the shock wave effect was minimised by careful manipulation of the grab. A standard technique was adopted whereby the grab was slowly lowered until it reached the bottom. It was then raised 1m and moved to one side of the original location and then allowed to fall freely onto the substrate. This allowed the grab to drop from a standard height onto a previously undisturbed substrate.

2. Cutting profile and penetration

The penetration of grabs into the substrate is related to their weight and to the nature of the substrate. When penetrating to the same maximum depth grabs that cut a near rectangle of material are more efficient than those that leave a mound of material behind or cut a profile with curved sides.

Underwater observations of the profile cut by the modified van Veen grab were not possible due to the poor visibility caused by the substrate disturbance. However, in areas where silt had accumulated the grab was observed to penetrate up to a depth of 12cm . On hard eroding clay shorelines no penetration was observed, only a scraping along the surface. Increasing penetration by the addition of weights was not attempted.

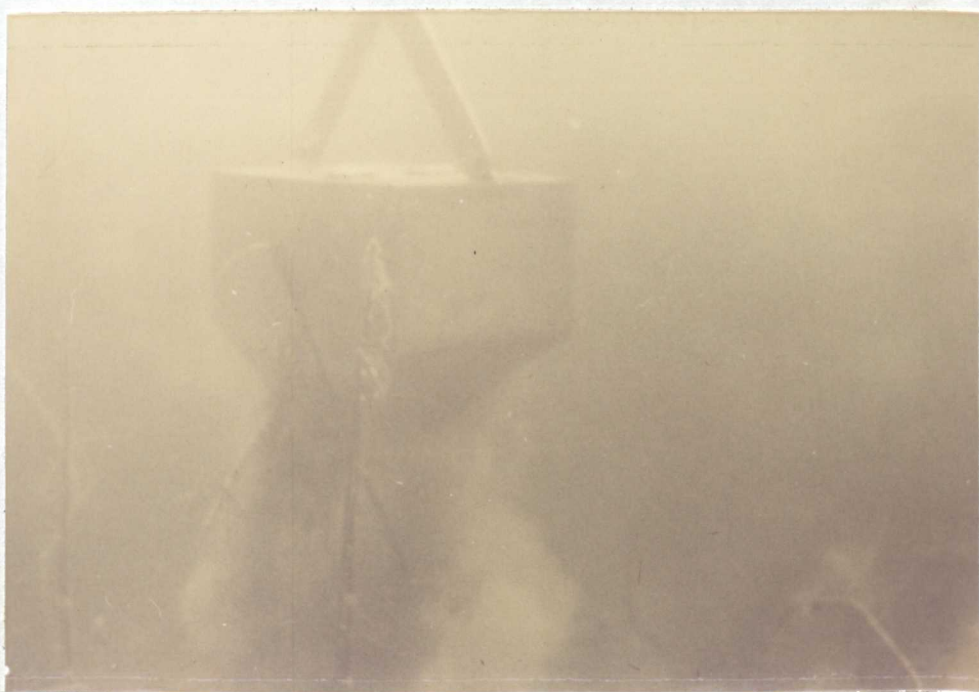
3.
and 4. Tilting side-on and end-on

Tilting of the grab when the jaws are closing may be caused by drifting of the boat or by one side of the grab failing

Plate 4. Underwater photograph of modified van Veen grab showing clouds of silt caused by shock wave.

Plate 5. Underwater photograph of modified van Veen grab showing unequal penetration of jaws.

Plate 6. Underwater photograph of modified van Veen grab showing loss of material on haul due to debris holding the jaws open.



to penetrate the substrate (Plate 5). This photograph also indicates that by lowering the grab carefully the shock wave effects can be minimised. Anchoring the boat each time a sample was taken prevented drifting and hence tilting of the grab.

5. Loss of material on haul

Loss of material whilst hauling the grab to the surface may be caused by stones or vegetation holding the jaws open (Plate 6). A standard Ekman grab with serrated jaws continued to lose material after hauling out of the water, whilst the modified van Veen grab did not. The Ekman grab serrations held material in one part of the jaws and allowed water and sediment to escape over the rest. The smooth cutting edge of the van Veen tended to squash and spread vegetation over the whole length of the cutting edge, thus forming a reasonable seal against further loss of material. Samples with the jaws partly open were disregarded and the sample retaken.

d) Comparison of modified van Veen, Ekman^M and Petersen grabs

A comparison was made of the profiles cut by these three grabs in a series of air/ground trials. The Ekman grab was used for sampling benthic invertebrates in this study and was fitted with a Rawson modification for automatic closure (Rawson, 1947). Compacted wet sand at the top of a sandy beach and loose dry sand on a sand dune system provided the hard and soft substrates on which to test the grabs. An area of level, undisturbed sand was chosen in each case. The operating mechanism of the grabs was set and each allowed to fall a height of 1m onto the substrate. The depth of penetration and profiles were recorded in each case.

The profiles and mean depth of penetration for each grab in each substrate are shown in Figure 15. On the hard substrate the modified van Veen and Petersen grabs cut profiles

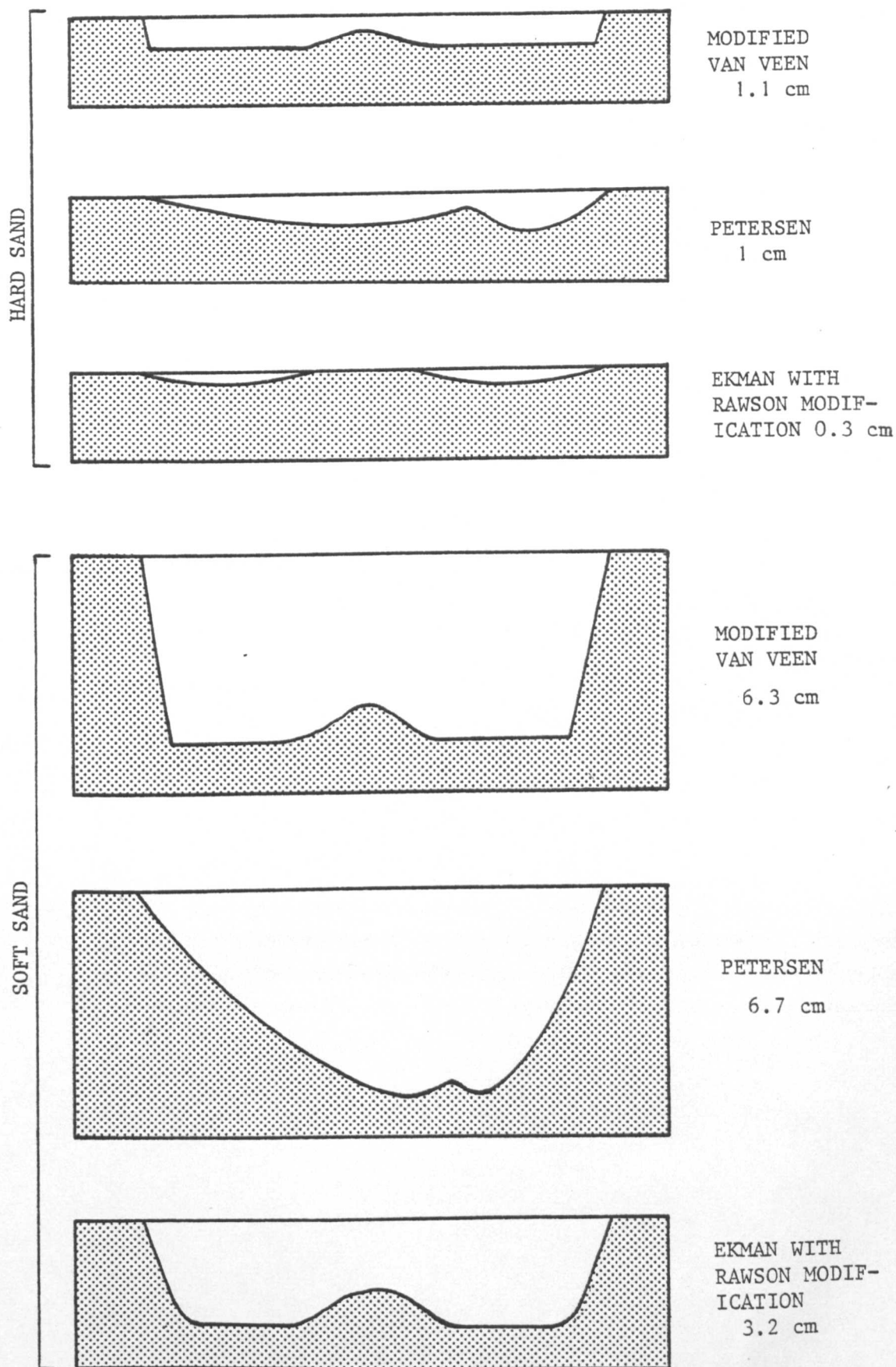


Fig. 15. Profiles and mean maximum depth penetration for three grab samplers.

to the same depth. The Petersen, however, cut in an arc and left a large mound of material where the jaws met. This was frequently off-centre as one jaw would bite deeper and result in the other moving towards it. The modified van Veen cut a more rectangular profile. The Ekman grab fitted with the Rawson modification was found to be very inefficient in this substrate. The paddles used to trigger the closure mechanism were set to operate before the base of the grab reached the substrate. This resulted in the premature closure of the jaws. The jaws cut in an arc and as the grab bounced upwards, due to the trigger mechanism, an uncut area of sand was left between the jaws (Fig. 15).

The profiles cut by the modified van Veen and Petersen grabs in soft sand were similar to those in the hard sand but with a greater depth penetration. The Petersen penetrated slightly deeper than the van Veen due to its greater weight. The Ekman grab cut a comparatively shallow profile due to the closure mechanism. However, this may not be the case underwater as in soft, flocculant sediments the paddles would penetrate to a greater depth before sufficient resistance is met to operate the closure mechanism. The Rawson modification is also thought to stabilise the grab when sampling, thus reducing the effects of tilting.

As both the modified van Veen and Ekman grabs were used for sampling benthic macroinvertebrates at Rutland Water, a direct comparison was made between the two by taking a parallel series of samples and comparing numbers of taxa, numbers of organisms and weight of substrate sampled. Each grab was used to take a sample from each of ten sites across the reservoir. After hauling to the surface each was emptied directly into a bucket. Samples were weighed and then washed through a 500 μ mesh sieve. All macroinvertebrates were removed, identified and counted.

Two of the ten samples produced identical numbers of taxa, four were higher for the Ekman and four for the van Veen (Table 2). The counts of organisms were corrected for the different sized grabs. The van Veen obtained larger numbers of Chironomidae, Gammarus, Oligochaeta and Hirudinea than the Ekman. The Ekman collected larger numbers of Asellus, Mollusca, Trichoptera and earthworms (Table 3). The total number of animals obtained from each grab was not significantly different at the 95% level using the Mann-Whitney U-test.

Neither of the two grabs consistently sampled a greater weight of substrate (Table 4). The difference between the substrate weights sampled was not statistically significant when using the Mann-Whitney U-test.

e) Sampling sites

The locations of four transects were defined on the basis of various landmarks by Bullock, at the eastern end of the reservoir (Fig. 16 NA, SA, D and T). One grab sample was taken at ten equidistant points along each transect. The points were determined by running the outboard engine at the same speed for the same period of time between points. In October 1977 the number of grab samples taken along the north-arm, south-arm and dam transects was increased from 10 to 12 to accommodate the increase in width of the reservoir due to filling. A standard Ekman grab was used from June 1976 to October 1977. From November 1977 to the end of the study the grab was used fitted with a Rawson modification (Rawson, 1947) for automatic closure.

Two transects located at the ends of the north and south-arms of the reservoir were sampled with the modified van Veen grab (Fig. 16 2NA and 2SA). One grab sample was taken at ten equidistant points along each transect. The location of the points was determined as described previously. The sampling schedule for the six transects is given in Table 5. The number of grab samples taken in four depth zones is also given.

Table 2: Number of taxa found in ten van Veen and ten Ekman grab samples

		Grab Number									
		1	2	3	4	5	6	7	8	9	10
Number of taxa	van Veen	5	7	4	8	6	3	5	2	7	9
	Ekman	4	7	6	4	7	3	6	4	3	7

Table 3: Number of organisms obtained in ten van Veen and ten Ekman grab samples

Nos. m ⁻²		
	van Veen	Ekman
Chironomidae	384	220
Gammarus	390	326
Asellus	323	348
Oligochaeta	333	321
Hirudinea	35	26
Mollusca	19	8
Trichoptera	0	44
Earthworms	0	4
Total	1,484	1,298

Table 4: Weight of substrate obtained in ten van Veen
and ten Ekman grab samples

Grab No.	Wt. of sample (kg m ⁻²)	
	van Veen	Ekman
1	36.8	25.5
2	9.8	14.1
3	21.3	24.6
4	13.9	25.0
5	15.0	22.2
6	26.9	13.0
7	15.2	16.5
8	20.2	19.9
9	12.2	0.8
10	6.8	1.1

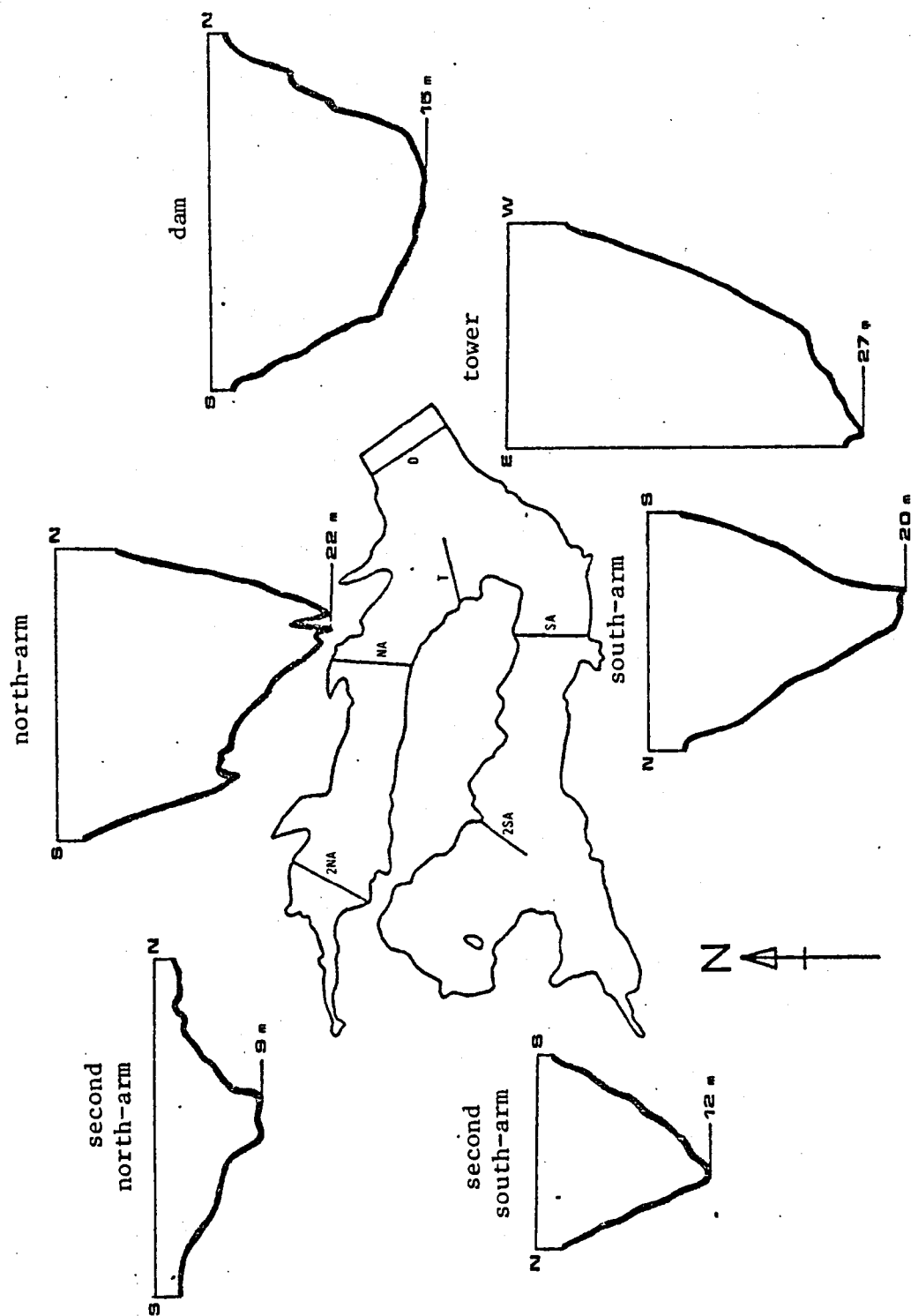


Fig. 16. Locations and profiles of transects.

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Table 5: Grab sampling schedule and number of samples from each depth zone.

Between June 1976 and September 1977 several qualitative collections were made using a dredge sampler. The dredge had an opening approximately 30cm wide and the material collected within a bag made of "Tygon" netting, mesh size approximately 1mm². The netting was retained within a wire mesh frame. The dredge was hauled for 50m along the same transects as the grab samplers. Two extra hauls were made running east-west along the north and south side of the central basin.// A pattern of random sampling or stratified random sampling was dismissed due to the size of the reservoir and the time involved in travelling between sites. The exchange arrangement with Leicester University enabled the chironomid larvae from up to 66 grab samples per month to be obtained. Brinkhurst (1974) suggests abandoning the single transect line as depth is not necessarily the dominant variable affecting distributions of organisms. This may be true in some situations but in a developing system such as a new reservoir where conditions are continuously changing no dominant variable such as substrate type can be established. Bearing in mind the constraints imposed by limited manpower resources, it was considered that one grab taken at ten equidistant points along each of six transect lines would provide a reasonably good estimate of the population density of the Chironomidae.

f) Sampling procedure

The modified van Veen grab was operated from the side of a 3m inflatable boat which was anchored at each site to prevent drifting. The grab was slowly lowered until it reached the bottom and then raised 1m before being allowed to fall freely as described above. The jolt on reaching the bottom releases the cross bar and the grab was slowly lifted, the jaws closing automatically. The water depth at each sampling point was noted. Grab contents were immediately emptied into a watertight bucket.

The following procedures were adopted by Leicester University and Leicester Polytechnic. Grab samples with stones or twigs caught in the jaws were discarded and retaken. At certain sites the bottom of the reservoir was covered in a dense mat of filamentous algae. Algae trailing from the jaws was trimmed to the edge of the grab.

g) Sorting procedure

Samples were stored in a cold room (4°C) until sieved. Approximately 90% of samples were sieved within 48 hours of sampling. Each sample was carefully sieved through a 500µm mesh sieve. The mesh size determines which instars of which species are retained in the sieve (Table 6). Although the 500µm sieve allows most first and second instars through, finer meshed sieves were not employed as standard practice due to the increased sieving and sorting time required.

The material from the sieve was washed into a translucent plastic tray (length 33cm, width 23cm) and illuminated by both incident light (60w) and transmitted light (40w). Flootation techniques were not employed due to the large amounts of organic material in the samples. Samples were sorted fresh as live moving animals are more easily detected. Systematic searches through the tray were made until no more animals were removed on three successive searches. Samples with large clay particles present required resieving at intervals to remove cloudy water caused by the searching action. Samples that contained large amounts of aquatic vegetation, mainly Cladophora and other filamentous algae, were subsampled. The algae were spread evenly in the tray and one quarter removed using scissors and forceps.

The use of forceps for removing larvae were restricted to the larger specimens. Small specimens were removed by means of an aquatic pooter (Fig. 17). This saved considerable time when removing large numbers of small animals. Animals were removed from the pooter by means of a small muslin filter and fine camel-hair brush.

Table 6: Larval head capsule widths of some chironomid species.

Species	Head capsule widths (μm)				Source
	1st Instar	2nd Instar	3rd Instar	4th Instar	
<i>Procladius choreus</i>	130-148	226-278	418-522	818-922	Potter & Learner 1974
<i>Psilotanypus ruffovittatus</i>	-	191-244	331-418	574-679	Potter & Learner 1974
<i>Ablabesmyia monilis</i>	90	150-175	325	575	Lindegaard & Jonasson 1979
<i>Cricotopus sylvestris</i>	75	125	200	350-375	Lindegaard & Jonasson 1979
<i>Orthocladius oblidens</i>	75-85	100-125	200	375	Lindegaard & Jonasson 1979
<i>Psectrocladius barbimanus</i>	85	150	275-300	525	Lindegaard & Jonasson 1979
<i>Chironomus plumosus</i>	113-122	209-261	452-522	853-1114	Potter & Learner 1974
<i>Glyptotendipes paripes</i>	-	191-244	365-470	731-905	Potter & Learner 1974
<i>Microtendipes</i> sp.	-	150	280	500	Carter 1976
<i>Parachironomus tener</i>	-	122-139	209-244	365-418	Potter & Learner 1974
<i>Polypedilum nubeculosum</i>	-	150	250	400	Konstantinov 1958
<i>Tanytarsus holochloris</i>	-	113-139	191-244	331-418	Potter & Learner 1974
<i>Tanytarsus gracilentus</i>	75	125-140	225-250	325-350	Lindegaard & Jonasson 1979

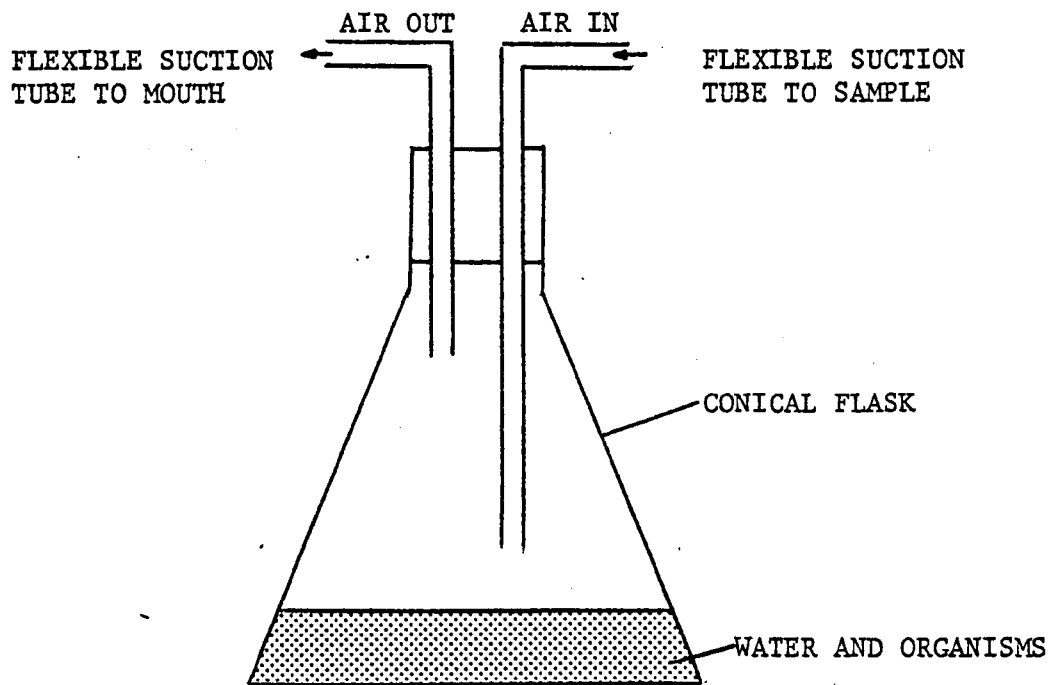


Fig. 17. Aquatic pooter used for removing small animals from samples.

A number of larvae removed from samples were reared to the adult for species identification. Animals were killed and preserved by immersion in 70% alcohol.

h) Number of sampling units in each sample

The dispersion of many species of benthic invertebrates is contagious and therefore large numbers of samples are required to calculate accurate population densities. In order to investigate the variability at one transect station 30 replicate grab samples were taken within an area of approximately 8m², and at a depth of 8m, in June 1978. Elliott (1971) suggests taking 5 sampling units at random and calculating the arithmetical mean. A further five sampling units are then added and the mean recalculated for the 10 samples. The results obtained using this method are shown in Table 7 and Figure 18. The optimum number of grab samples for this particular station is between 5 and 10 to obtain an estimate of the population density for the Chironomidae taken as a group. However, new taxa were still being recorded after 20 samples had been taken (Fig. 18).

Using the formula:

$$n = \frac{S^2}{D^2 \bar{x}^2}$$

where n = number of sampling units, S² = variance, \bar{x} = mean and D = level of required accuracy, the number of grab samples required to estimate the population for a specified degree of accuracy can be calculated (Elliott, op. cit.). For a standard error of 20% of the mean, 20 samples were required. If a negative binomial distribution is assumed and a rough estimate of the common k in the negative binomial series is calculated using the formula:

$$k = \frac{\frac{\bar{x}^2}{S^2 - \bar{x}}}{S^2 - \bar{x}}$$

then the number of sampling units can be calculated using the

Table 7: Effect of increasing the number of sampling units
on the calculate mean population density of
chironomid larvae.

a. One transect station

Number of Sampling Units (grabs)	Mean Number of Chironomid larvae per grab	Standard Deviation
5	8.0	7.38
10	10.2	6.37
15	10.1	5.39
20	9.7	4.93
25	9.2	5.35
30	10.6	9.52

b. Whole reservoir

Number of Sampling Units (grabs)	Mean Number of Chironomid larvae per grab	Standard Deviation
5	12.8	19.24
10	8.9	13.86
15	6.4	11.78
20	4.9	10.47
25	5.0	9.78
30	5.7	10.23
35	5.6	9.71
40	5.2	9.22

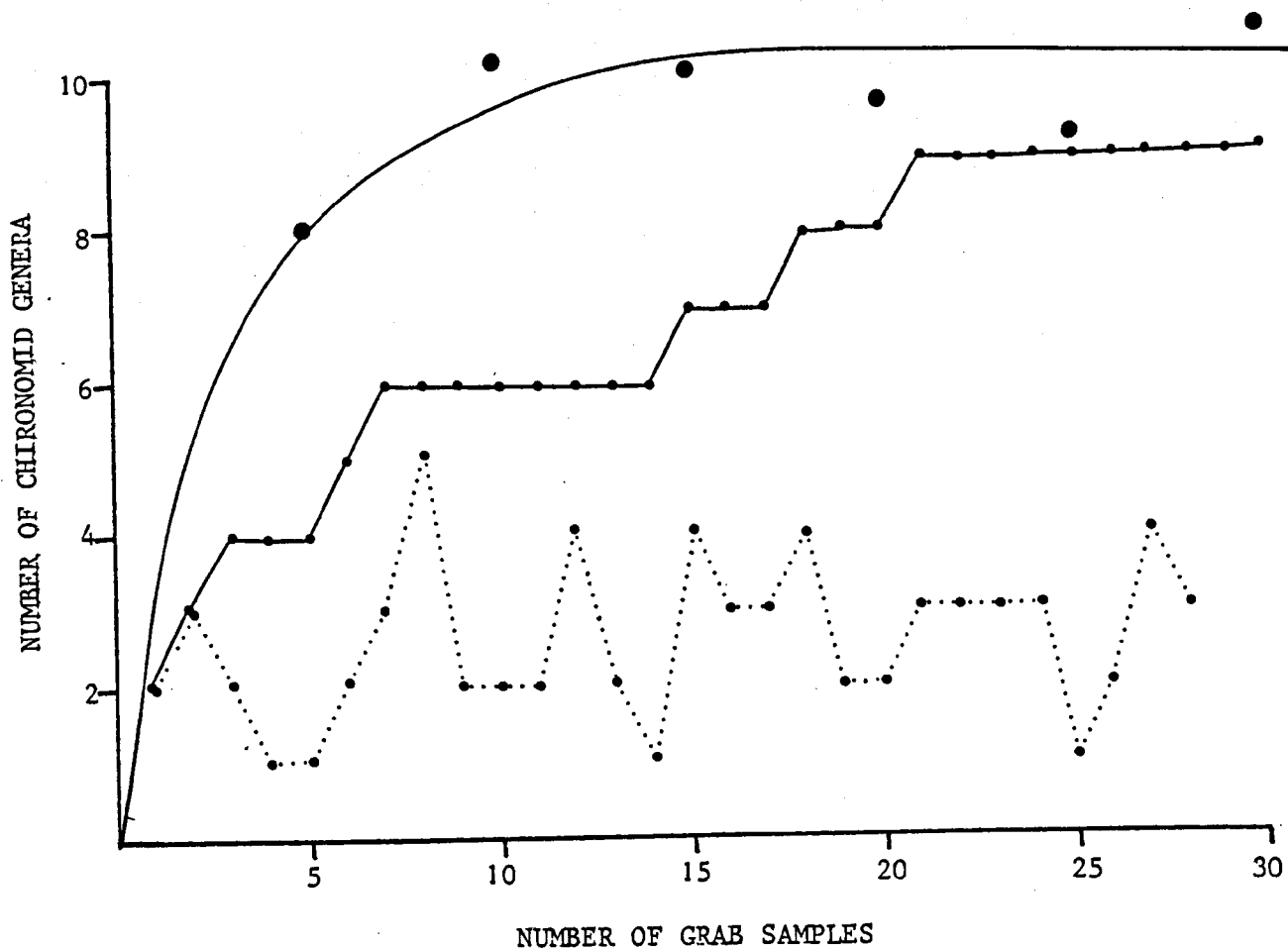


Fig. 18. Effect of increasing number of sampling units (grab samples) at one transect station.

● mean population per grab, recalculated at five sampling unit intervals; ●.....● Number of genera per grab; ●——● cumulative number of genera.

formula:

$$n = 25 \left(\frac{1}{\bar{x}} - \frac{1}{k} \right)$$

Approximately 16 grab samples are required from this station for a 20% error of the population mean.

However, these estimates will vary at each station, different depths, times of year and for different species. For example, calculating the number of sampling units accepting a 20% error of the population mean and assuming a negative binomial, gives values of 17 sampling units for Procladius larvae and 27 sampling units for Chironomus larvae.

In order to estimate the variance in chironomid population densities over the whole reservoir, 40 grab samples were taken in September 1977 from the tower, dam, north-arm and south-arm transects (Fig. 16) and analysed. The method of calculating means at five sampling unit intervals was adopted. The results (Table 7) indicate that less than 10 grab samples do not give an accurate estimate of the mean population density. Little fluctuation in this value occurred between 15 and 40 grab samples.

Spatial or temporal comparison of single grab samples taken along each transect is not possible as reliable estimates of the standard errors cannot be made, nor are the samples taken at exactly the same site each month. Spatial comparisons can be made by treating all the grab samples as one sample composed of up to 66 sampling units. The variance may be reduced by dividing the sampling units into different depth zones and treating each as separate samples.

Computing

Data on chironomid larvae obtained from grab samples were analysed using SPSS (statistical package for the social sciences) on a Burroughs 6700 computer. The application of SPSS to the survey data is described in Appendix A.

Identification and Rearing of Chironomid Larvae

Chironomid larvae were prepared for identification by separating the head capsule from the body. Dark heavily chitinised head capsules were boiled in 10% potassium hydroxide to remove internal tissues and to clear them. The head capsules were mounted ventral side up, next to the body under one coverslip. Polyvinyl-lactophenol was initially used as the mounting medium, but this may distort the specimen due to shrinkage. Berlese fluid was subsequently used as this causes less shrinkage. A detailed description of the techniques for mounting chironomid larvae has been provided by Cranston (1977).

Until 1977 several keys were used for the identification of larvae. The Chironominae and Tanypodinae were identified using the keys by Bryce (1960) and Bryce and Hobart (1972). A key by Chernovskii (1949) and two translations of part of the key by Pankratova (1949) were used for the identification of the Orthocladiinae. A provisional key to the genera of the British chironomid larvae (Cranston, 1977) was obtained in 1977 and was used for all later identifications. Larval identifications were confirmed by Cranston (British Museum (Natural History)).

Certain species identifications were confirmed by rearing to the adult male stage, the identification of which will be referred to in a subsequent section.

Two techniques for rearing larvae were evaluated. The first method involved placing fourth instar larvae individually into 100ml beakers, to which a little tap water and sediment had been added for tube building and food. The beakers were left at room temperature (14-18°C). Approximately 50% of the larvae either did not emerge or died. Slightly better results were obtained by aerating the water. The containers, although bulky, were easy to stack. When they became infected with fungi they required careful cleaning as larvae are vulnerable to infection.

The second technique, adopted for most of the study, involved the use of 5cm diameter plastic disposable petri dishes. Individual larvae were placed in these with tap water. This was thought to be preferable to distilled water as the chlorination process to which tap water is subjected reduces fungal infection (Langton, pers. comm.). Reservoir water was not used as it was thought likely to contain fungal spores. The petri dishes used had a sufficiently large surface area to allow oxygen diffusion into the water without the need for aeration. They are also cheap and easy to stack. Mortality of the larvae and non-eclosion may be further reduced by rearing in a temperature and light controlled incubator set as close as possible to the conditions from which the larvae were obtained (Cranston, pers. comm.).

Collection and Identification of Pupal Exuviae

Cast pupal skins were collected at a number of sites around the reservoir, depending on wind strength and direction, at approximately fortnightly intervals. Samples of wind driven foam or plant debris were taken by hand and placed in a bucket fitted with a watertight lid. All samples were collected between 11 am and 1 pm. The material was sorted by hand in the laboratory and preserved in 70% alcohol to which a few drops of glycerol had been added.

Slides were prepared by mounting the skin dorsal surface uppermost in polyvinyl-lactophenol or Berlese fluid. Several skins may be placed under one coverslip for examination and comparison. Exuviae were identified using Wilson's (1978) provisional key to genera.

Collection and Identification of Adults

Adults were collected by means of a fine mesh sweep net from sites around the reservoir when conditions were favourable for the formation of mating swarms. Adults were killed in ethyl acetate vapour and preserved in 70% glycerol alcohol.

A quick technique for mounting the male adults on slides was adopted for routine examination. The head, antennae, legs and wings were mounted together with the thorax on a slide and covered with a 22 x 32mm coverslip. The hypopygium was mounted separately under a 6mm diameter coverslip. This enables correct orientation of the structure. A more detailed description of the techniques for the preparation of slides may be found in Pinder (1978).

Prior to 1978, keys by Coe (1953), Fittkau (1962), Reiss and Fittkau (1971), Hirvenoja (1973) were used for the identification of adult males. In 1978 a key to the adult males of the British Chironomidae was published (Pinder, 1978) and was used for all subsequent identifications.

Collection and Treatment of Fish Stomachs

During the fishing season, April to October 1977, stomachs from both bank caught and boat caught, brown and rainbow trout were collected from fishermen by Warlow (Leicester Polytechnic). In the close season trout stomachs were removed from fish obtained in purse seine and beach seine nets.

The alimentary canal was exposed after a median ventral incision had been made in the body wall from the cloaca forward to the gill arches. The anterior end of the cardiac portion was severed behind the buccal cavity and the posterior end of the intestine was severed at the junction with the cloaca. The gut was then removed from the body cavity and preserved in 5% formalin. Where the contents of the stomach and intestine were studied separately a cut was made just posterior to the pyloric sphincter.

The stomach was cut longitudinally and any food was removed and preserved in 70% alcohol. Chironomid larvae, pupae and adults were isolated from other items and studied separately. The stomach contents were dried at 105°C until a constant weight was achieved.

CHAPTER 4

DEVELOPMENT OF RUTLAND WATER

Water Chemistry

a) Chemical features of the rivers and reservoir

The River Nene has the largest catchment area of the three water sources of the reservoir. A number of towns are located within the catchment and sewage effluent input to the river is high (Table 8). The rivers Welland and Gwash carry mainly agricultural drainage with less sewage effluent than the Nene. The major chemical characteristics of the rivers Welland and Nene and the reservoir are shown in Table 9. The River Nene has the highest levels of electrical conductivity, and the highest concentrations of nitrate and total phosphorus. Chlorophyll-a levels are also highest in the Nene. The River Welland carries more suspended solids than the Nene probably due to the higher proportion of agricultural drainage (Harper, pers. comm.).

Concentrations of the major ions in the rivers and the reservoir are given in Table 9. Calcium is the dominant cation and bicarbonate is the dominant anion. Bicarbonate was measured as the carbonate alkalinity and therefore includes the CO_3^{2-} anion. Water derived from the marl soils in the catchment area is high in sulphate and therefore both the rivers and the reservoir have high concentrations of sulphate ions. Generally the rivers are chemically comparable with other lowland rivers such as the Thames (Youngman, 1975) and the Great Ouse (Toms *et al.*, 1975).

b) Physical and chemical changes in the reservoir

The period of study can be divided into four phases in terms of water level. A period of rapid filling from January 1975 to April 1975; a period of stable water level from April 1975 to September 1976; a second phase of rapid filling from September 1976 to May 1977, and finally a relatively stable

Table 8: Physical data on water inputs to reservoir (from Anglian Water Authority data)

	R. Gwash	R. Welland	R. Nene
Mean daily flow rate 1975-1978 ($1 \text{ day}^{-1} \times 10^6$)	-	4.95	14.16
Catchment area (km^2)	75	531	1,582
Sewage works output ($\text{m}^3 \text{ day}^{-1}$)	Oakham 2,050	Market Harborough 9,000	Northampton Daventry Welling- borough 117,000

Table 9: Major physical and chemical characteristics of the rivers and reservoir outlet. Mean weekly values for 1975 to 1978 calculated from data provided by Anglian Water Authority.

	R. Welland (Tinwell)	R. Nene (Wansford)	Reservoir (Outlet)
Temp ($^{\circ}\text{C}$)	10.69	10.60	10.75
pH	8.14	8.21	8.27
Diss. oxygen (mg l^{-1})	11.19	11.38	9.36
Elect. conductivity ($\mu\text{S cm}^{-1}$)	824.76	1087.20	783.75
Total susp. solids (mg l^{-1})	54.99	20.35	8.87
Nitrate (mg l^{-1})	8.33	11.00	4.08
Total phosphate (mg l^{-1})	0.37	0.93	0.14
Diss. silica (mg l^{-1})	4.54	5.31	2.22
Ca^{2+} (mg l^{-1})	126.90	148.10	116.70
Mg^{2+} (mg l^{-1})	12.30	12.10	11.50
Na^{+} (mg l^{-1})	34.20	7.400	37.00
K^{+} (mg l^{-1})	7.90	14.80	8.90
Fe^{2+} (mg l^{-1})	0.45	0.63	0.27
SO_4^{2-} (mg l^{-1})	158.50	204.70	161.50
HCO_3^{-} (mg l^{-1})	192.50	207.20	179.30
Mn^{2+} (mg l^{-1})	0.029	0.054	0.150
Cl^{-} (mg l^{-1})	48.90	90.00	54.20
Chlorophyll-a (mg m^{-3})	7.92	44.91	8.98

period from May 1977 to the end of the study period, April 1979 (Fig. 9). During the filling period water was derived in different proportions from each of the three main sources (Fig. 10). The resulting physical and chemical changes reflect the intermittent filling regime, the origin of the water, as well as the seasonal patterns and processes of succession.

i) Water temperature and dissolved oxygen

Weekly surface water (0.5 m deep) temperatures (Fig. 19) were recorded by the Anglian Water Authority at the reservoir outlet (Fig. 12) from March 1975 to April 1979. The highest temperature, 23°C , was recorded in August 1975. Relatively low air and water temperatures were recorded in the summer months 1977 and 1978.

Dissolved oxygen concentrations (Fig. 19), from the same site, show a general inverse relationship to temperature throughout the period. Despite the highest temperatures being recorded in 1975, however, the level of dissolved oxygen only fell to 7 mg l^{-1} . Levels of 2.5 mg l^{-1} and 2.8 mg l^{-1} were recorded in July 1976 and July 1977 respectively.

The reservoir is isothermal for most of the year (Fig. 20). In 1975 a thermocline occurred from June to August and in 1976 from June to September. Incomplete data for 1977 indicate that a thermocline was beginning to form in June, as in the previous two years, although the extent and duration is unknown. In 1978 a thermocline began developing in June. The helixor air guns came into operation to disrupt this thermocline but it is thought that it was largely destroyed by a gale later in the month (Ferguson, pers. comm.). In 1975, 1976 and 1977 levels of dissolved oxygen fell in the hypolimnion to less than 40% saturation in June and July (Harper, 1978).

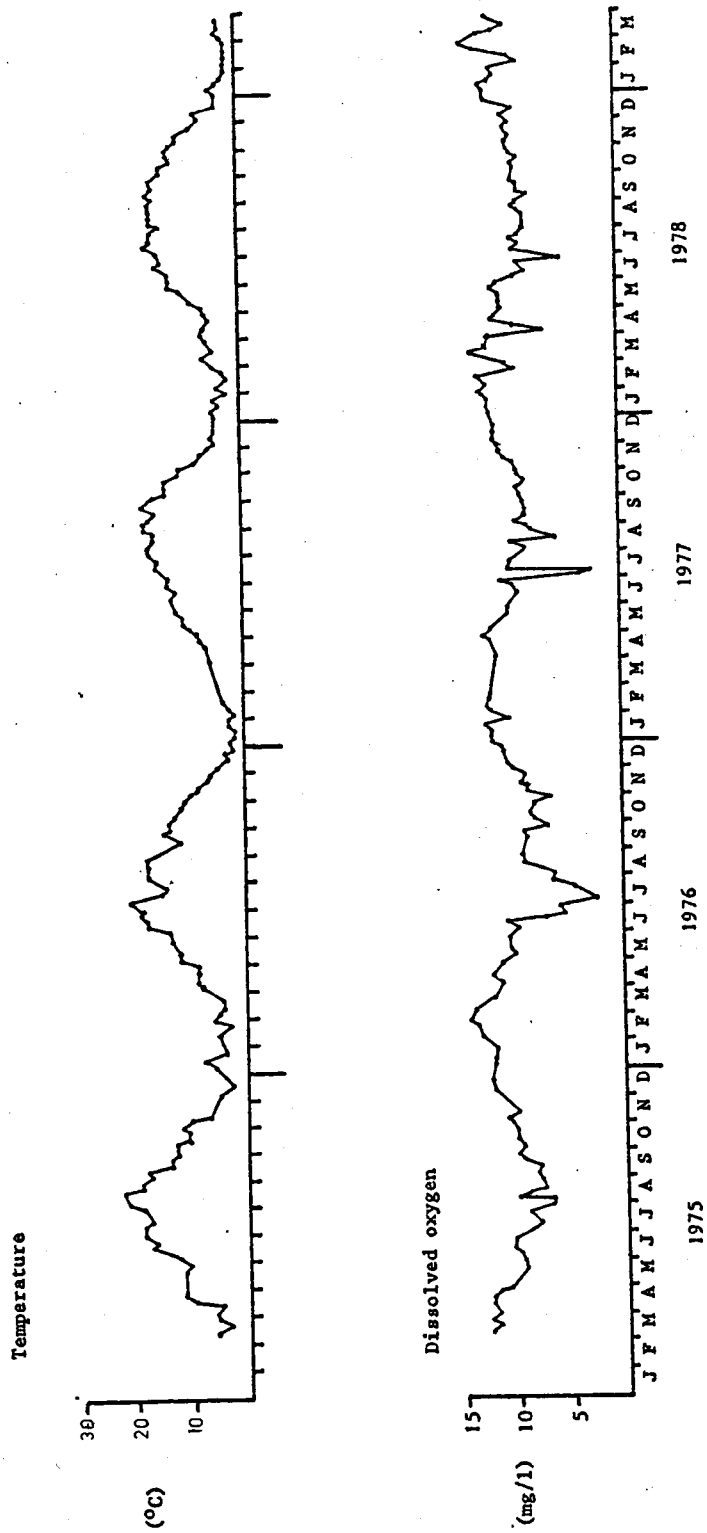
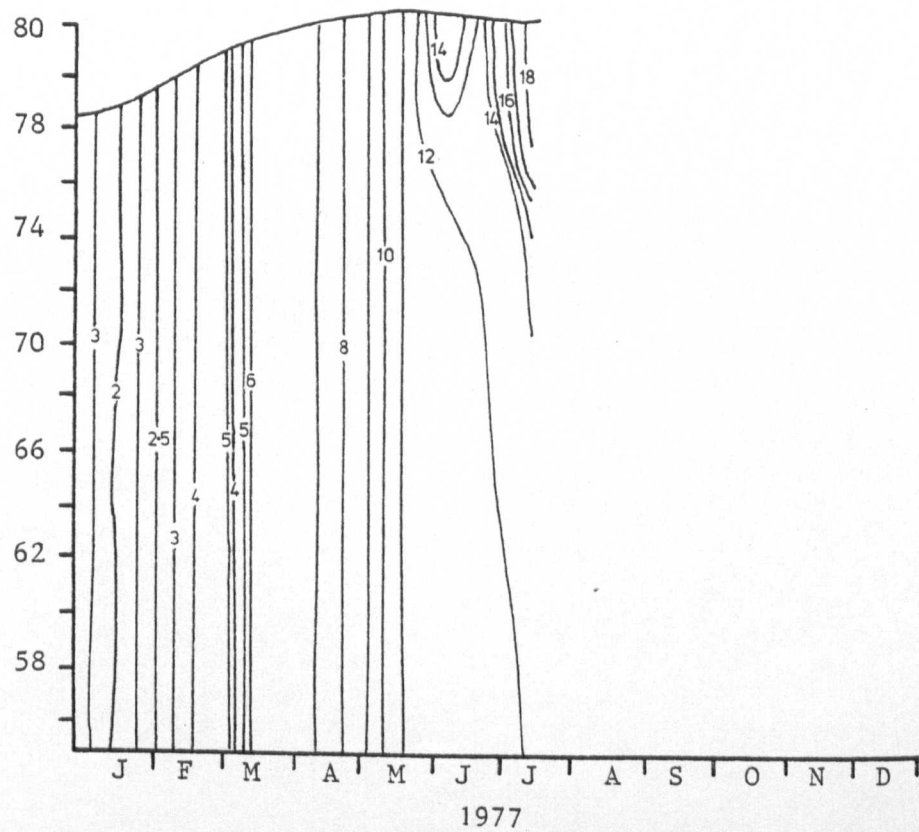
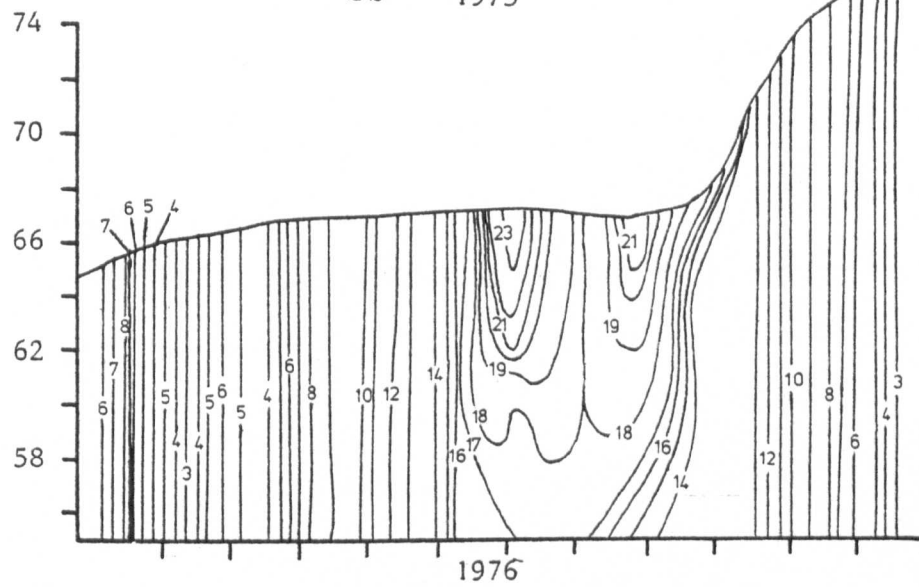
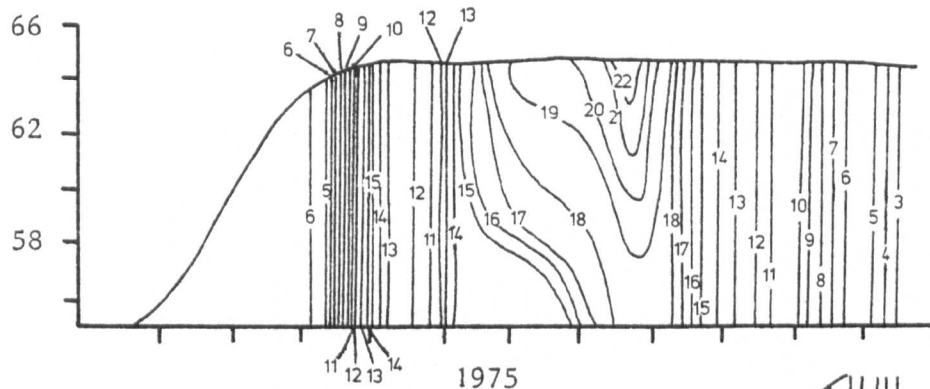


Fig. 19. Seasonal variation in surface water temperature and dissolved oxygen taken at the reservoir outlet (from data by A.W.A.)

METRES ABOVE O.D.



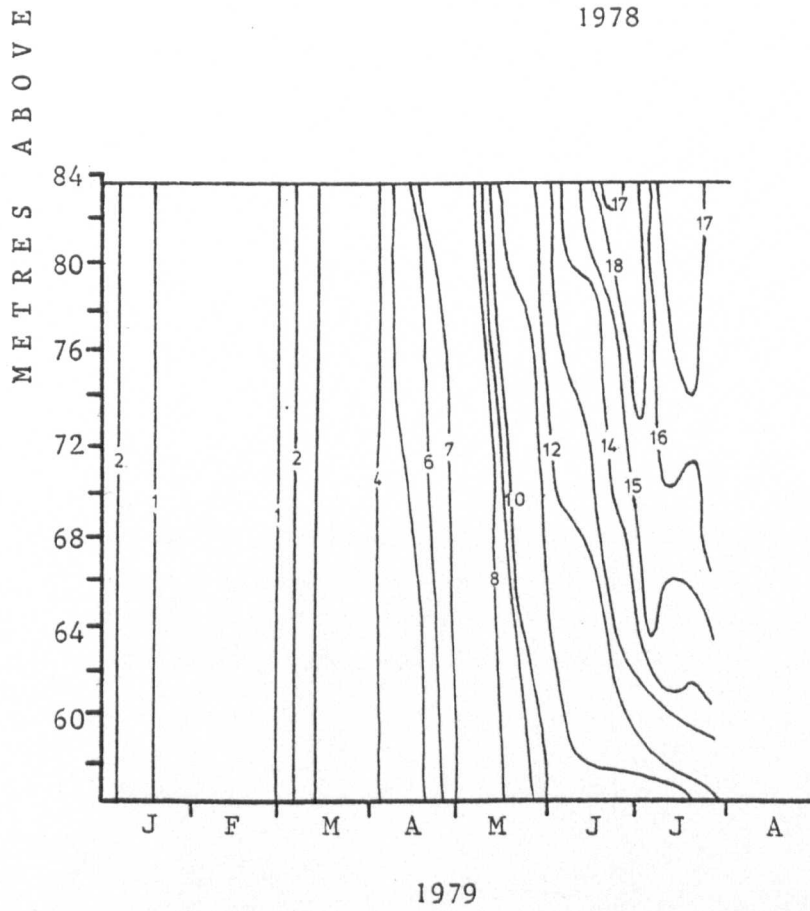
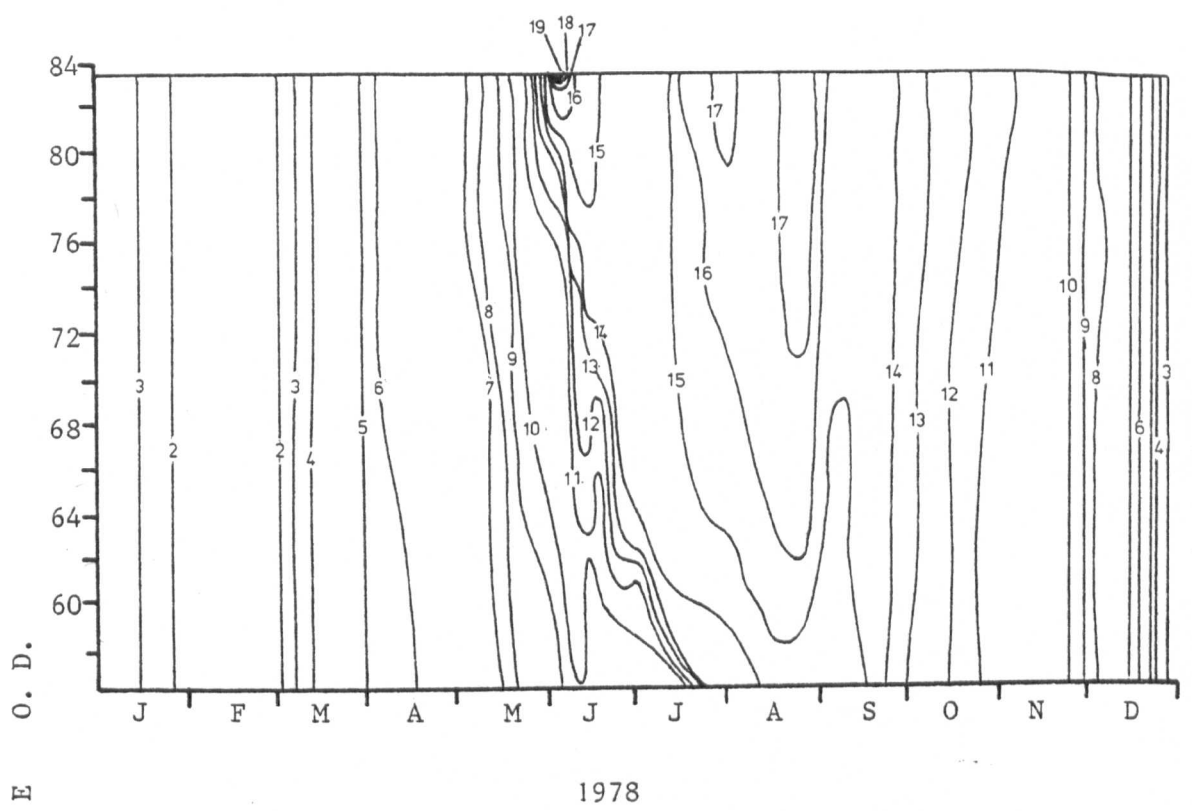


Fig. 20. Vertical temperature profiles in the central basin. (1975, 1976 & 1977 from Harper 1978; 1978 & 1979 provided by A.W.A.). Isoleths at 1°C intervals.

Due to the shape of the reservoir physical conditions are frequently very different between the two arms and the central basin. This is caused by the effect of the peninsula sheltering the north arm from the prevailing winds. Harper (1978) recorded a 3°C difference in surface water temperature between the arms and the central basin. Although not stated by Harper this is presumably caused by wind induced water circulation.

ii) Temporal changes in water chemistry

Samples of water from the outlet site (Fig. 12) were analysed at approximately weekly intervals by the Anglian Water Authority throughout the study period. All samples were collected during the morning to avoid differences due to time of sampling. pH showed little fluctuation and remained within the range 7.7-8.8 (Fig. 21). Carbonate alkalinity showed large fluctuations in March 1975 and again in July and August 1976 (Fig. 21). From May 1977 to the end of the study period the value remained fairly constant at approximately 180 mg l⁻¹.

Electrical conductivity (Fig. 21) showed a dramatic increase from less than 600 μ S cm⁻¹ in the early part of 1975 to a maximum of 1,080 μ S cm⁻¹ at the end of 1976. The value fell during 1977 and remained relatively constant throughout 1978; mean 782 μ S cm⁻¹, range 715-860 μ S cm⁻¹. Increases in the concentration of nitrate and phosphate coincided with the increases in electrical conductivity. The concentrations of these nutrients increased on each occasion that river water was pumped into the reservoir (Fig. 21). Further data on the periods of pumping and the origin of the water are given in Figure 10. Peak concentrations of nitrates occurred in January 1977, 11.6 mg l⁻¹ (Fig. 21). The concentration then fell gradually to a value of approximately 3 mg l⁻¹ in January 1979. Phosphate concentrations showed a similar trend.

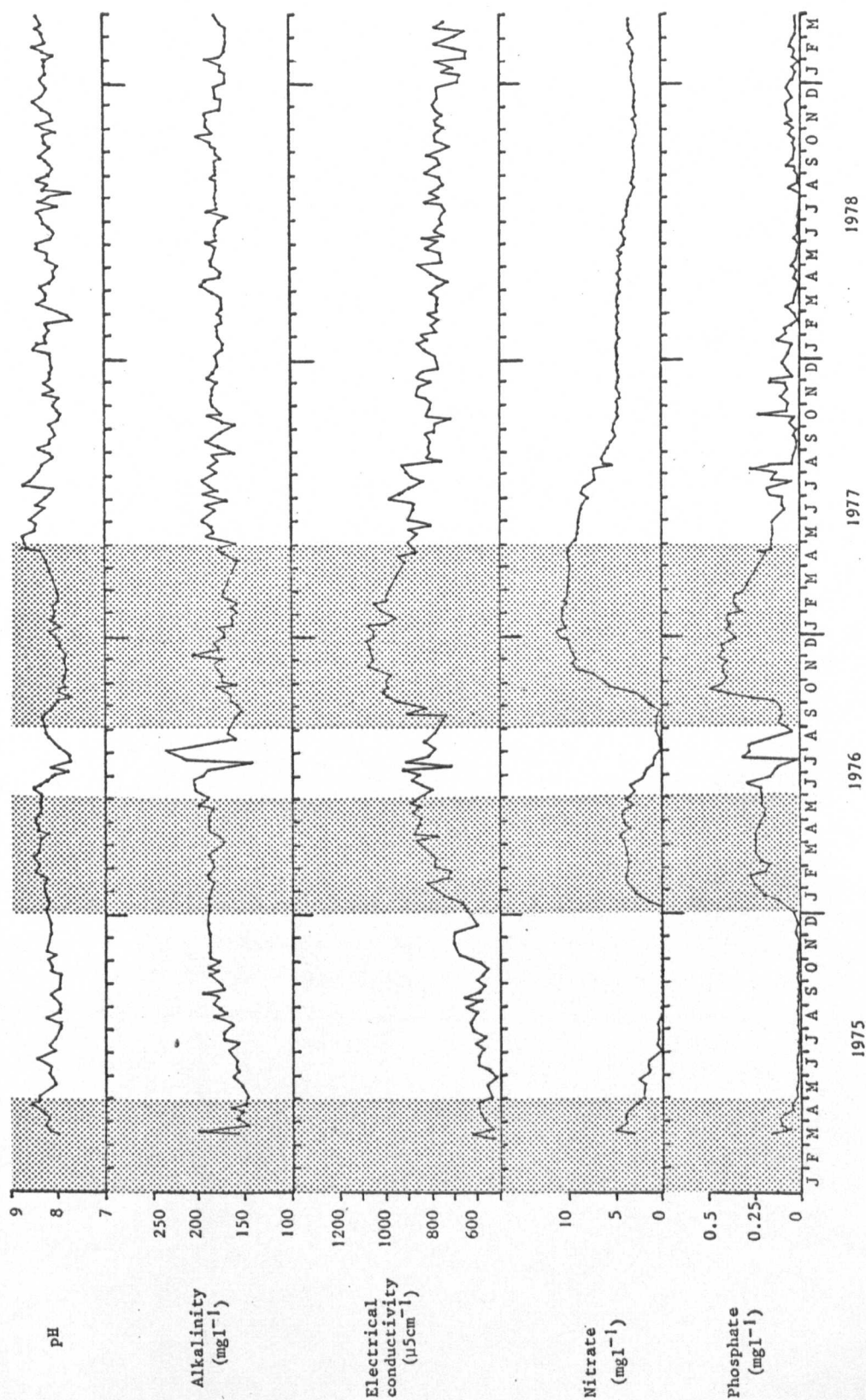


Fig. 21. Variation in the major chemical characteristics. Samples taken from the outlet site. Stipled area: periods of water level rises.

Harper (1978) reports that until the middle of 1977 nitrate was derived in almost equal amounts from the River Nene (33%), the River Welland (35%) and the River Gwash (26%). Phosphate came mainly from the River Nene (55%) and the northern tributary of the River Gwash (26%). A further 12% came from the River Welland and 7% from the southern tributary of the River Gwash.

iii) Spatial differences in water chemistry

A number of factors probably affect water quality within the reservoir. Amongst the more important are probably the supply of river water to the south-arm, the entry of treated sewage effluent into the south-arm and the wide expanse of shallow water at the western end of the south-arm and the area behind the bunds which support large flocks of water fowl. These may contribute significant amounts of nutrient from guano as found in other lakes by Leentvaar (1967) and Brinkhurst and Walshe (1967).

The major chemical characteristics of the water were compared from five sites around the reservoir in 1978 (Table 10). No clearly observable differences in these mean values for 1978 can be identified. Two sites were chosen at the western ends of the north-arm and south-arm of the reservoir that were expected to show the maximum differences in water chemistry. Monthly means for temperature, electrical conductivity, nitrate and phosphate concentrations were compared (Table 11) but little difference was observed. Whilst the values were rarely the same at the two sites the differences were not statistically significant using the Mann-Whitney U-test.

c) Discussion

As expected, Rutland Water has become a eutrophic reservoir (Harper, 1978). Nutrient input from the rivers was $26 \text{ g m}^{-2} \text{ N}$ and $1 \text{ g m}^{-2} \text{ P}$ in 1975 and was 3-4 times higher in 1976 and 1977

Table 10: Chemical data from five sites (refer to Fig. 12) sampled weekly throughout 1978. Mean \pm standard error. (Data from Anglian Water Authority)

	North-arm (N1)	North-arm (N2)	Outlet	South-arm (S10)	South-arm (S13)
(mg l ⁻¹)					
Alkalinity CaCO ₃	176 \pm 2.31	178.5 \pm 1.83	180.8 \pm 0.98	177.7 \pm 1.48	180.3 \pm 1.48
Electrical conductivity (μ S cm ⁻¹)	791.6 \pm 7.79	775.3 \pm 11.21	779.9 \pm 5.12	784.7 \pm 8.13	796.1 \pm 7.71
Nitrate	4.05 \pm 0.28	3.88 \pm 0.23	3.66 \pm 0.23	3.91 \pm 0.23	4.04 \pm 0.37
Diss. phosphate	0.037 \pm 0.008	0.036 \pm 0.008	0.051 \pm 0.007	0.039 \pm 0.009	0.036 \pm 0.01
Calcium	11.61 \pm 1.10	116.7 \pm 1.19	115.6 \pm 1.06	116.8 \pm 1.23	116.3 \pm 1.23
Magnesium	11.5 \pm 0.09	11.8 \pm 0.22	11.6 \pm 0.10	11.6 \pm 0.09	11.6 \pm 0.09
Sodium	39.4 \pm 0.37	39.9 \pm 0.54	40.2 \pm 0.52	39.4 \pm 0.65	39.2 \pm 0.74
Potassium	9.1 \pm 0.57	8.9 \pm 0.26	8.8 \pm 0.15	9.9 \pm 0.42	8.7 \pm -
Chloride/chlorinity	57.4 \pm 0.40	56.9 \pm 0.75	57.8 \pm 0.55	57.0 \pm 0.49	57.3 \pm 0.67
Sulphate	170.1 \pm 0.99	170.0 \pm 0.62	170.8 \pm 0.93	160.7 \pm 11.45	165.7 \pm 7.22

Table 11: Mean weekly values of physical and chemical characteristics at two sites at the end of the north-arm (N1) and the south-arm (S13). Refer to Figure 12 for locations.

Date	Temperature (°C)		Electrical Conductivity ($\mu\text{S cm}^{-1}$)		Nitrate (mg l^{-1})		Phosphate (mg l^{-1})	
	N1	S13	N1	S13	N1	S13	N1	S13
28. 6.77	13.8	13.7	-	-	7.7	7.8	0.081	0.081
9.. 8.77	17.0	17.5	850	860	6.4	6.4	0.027	0.027
6. 9.77	15.8	15.8	810	810	5.57	5.21	0.027	0.027
4.10.77	13.0	13.0	810	800	4.97	4.96	0.03	0.03
1.11.77	11.0	10.9	800	800	4.44	4.57	0.03	0.05
29.11.77	4.5	4.0	805	810	4.48	4.35	0.067	0.067
13.12.77	5.5	5.0	840	830	4.3	4.39	0.04	0.05
4. 1.78	4.0	4.0	800	820	4.5	4.48	0.081	0.094
30. 1.78	2.8	2.6	835	840	4.64	4.67	0.081	0.067
28. 2.78	4.0	3.5	805	805	4.75	4.65	0.035	0.072
29. 3.78	6.5	-	765	-	4.37	-	0.027	-
25. 4.78	8.0	7.5	805	795	4.14	5.56	0.03	0.03
23. 6.78	11.0	11.5	810	800	4.39	4.10	0.013	0.03
20. 6.78	14.8	16.5	815	825	6.05	5.47	0.02	0.02
18. 7.78	16.5	16.5	755	765	3.5	3.39	0.02	0.027
15. 8.78	16.0	16.0	745	765	3.09	2.98	0.02	0.02
10.10.78	12.5	12.5	780	780	3.57	2.84	0.013	0.13
7.11.78	10.5	10.5	810	800	3.03	2.79	0.081	0.94

(Harper, op. cit.). Concentrations of nitrate and phosphate were higher than those recorded in Chew Valley and Blagdon reservoirs (Wilson et al., 1975) but lower than those recorded in Farmoor (Youngman, 1975) or Grafham reservoirs (Toms et al., 1975).

Impounded river water undergoes a series of changes both in chemical composition and in biological activity (Symons, 1969; Toms et al., 1975). A comparison of the chemical composition of the rivers Welland and Nene with the reservoir indicates a considerable reduction in most of the major ions including nitrate and phosphate. However, accurate estimates of the loss of nutrients to the lake sediments and nutrient budgets have not been made. As a rough estimate approximately 600-700 tonnes of nutrients have been lost in the sediments between 1971 and 1979 (Ferguson, pers. comm.).

Seasonal changes in the concentration of nitrate, phosphate and silica have been recorded in a number of temperate lakes (Heron, 1961). In Grafham reservoir concentrations of nitrate and silicate were found to be low in summer, whilst phosphate reached its lowest level earlier in the season (Toms et al., 1975). In Rutland Water seasonal cycles in the concentration of nutrients are confused by the intermittent pumping of river water into the reservoir. Harper (1978) reports that seasonal fluctuations in nitrate and phosphate concentrations in the reservoir in 1976 and 1977 were typical of temperate impoundments. However, when the times of pumping of river water into the reservoir are studied they are found to coincide closely with the observed rises in concentrations of these nutrients. This suggests that the pumping of nutrient rich river water into the reservoir and subsequent decomposition of flooded terrestrial vegetation during the filling phases was more important in accounting for the observed increases in nitrate and phosphate than were seasonal fluctuations of nutrients. This idea is supported by the comparatively small fluctuations in these nutrient concentrations that occurred in 1978 when little water was pumped into the reservoir.

There has been little experimental work on the fate of nitrogen compounds in lakes and reservoirs. The observed decline in concentration of nitrate may be due to several factors; sedimentation after assimilation by algae and macrophytes; bacterial denitrification; export from the system by wave action. Vollenweider (1968) reports that the rate of nitrogen loss in various Swedish lakes was between $0.005-0.56 \text{ g m}^{-1} \text{ day}^{-1}$. In Lake Mendota Brezonik and Lee (1968) estimated that sedimentation accounted for 67% of the total nitrogen input and denitrification only 11%. Denitrification has been as high as one-third of the total nitrogen input in some lakes (Kuznetsov, 1968). At Rutland Water anaerobic conditions are not generally maintained for very long and hence the importance of denitrification in removing nitrogen will be reduced. However, the nutrient rich pumped river water may contain high bacterial numbers which would increase the loss of nitrate by denitrification. As far as the author knows the third possible mechanism for the removal of nitrates has not been studied. It is known that some nutrients may become concentrated in the surface film (Thomas, pers. comm.) and these nutrients may be removed from the system during wave action along the shoreline.

Phosphates are lost from the system by chemical precipitation and by uptake by algae and plants (Toms et al., 1975) and possibly wave action on the surface film. Compared to nitrate the slightly more rapid decrease in phosphate concentration during storage may be attributable to the removal and storage mechanisms employed by algae (Mackereth, 1953).

Algae

a) Succession of major planktonic species

In spring 1975, a period of rapid natural filling (Fig. 9), large populations of Micratinium pusillum, Thalassiosira sp. and Chroococcus dispersus developed. These declined in April and May

and low algal populations were maintained throughout the summer months (Fig. 22). In 1976 and 1977 a seasonal pattern of species succession and algal biomass developed (Harper, 1978). The major spring bloom was dominated by the diatom Stephanodiscus astraea and the population was probably limited by silica depletion. The summer/autumn bloom was dominated by Aphanizomenon flos-aquae and this population was probably limited by light. In a eutrophic reservoir such as Rutland Water the concentrations of nitrate and phosphate are not usually the major factors limiting algal growth and in 1976 and 1977 the concentrations of these nutrients were in excess of algal requirements (Harper, op. cit.).

In 1978 the spring bloom was dominated by Thalassiosira sp. and relatively low algal standing crops, as measured by chlorophyll-a, were recorded during the rest of the year (Fig. 22). Aphanizomenon flos-aquae and Anabaena circinalis were again dominant during the autumn months. In spring 1979 a mixed algal community appeared which included blue-green algae as well as the expected diatoms.

b) Vertical and horizontal distribution

The spatial distribution of algae is of particular importance in the management of reservoirs due to the problems of abstraction and subsequent treatment of water with high algal standing crops. From 1975 to 1977 Harper (1978) observed little difference in the vertical distribution of algae except in late summer and early autumn. In September 1976, for example, 263 mg m^{-3} chlorophyll-a was recorded at the surface and only 4 mg m^{-3} at 6m depth.

Until April 1977 no significant horizontal variation in phytoplankton was observed by Harper (1978). At the end of April, however, the spring diatom bloom began to decline in the central basin but was maintained in the two arms. This was thought to be due to the influx of silica from the two tributary

streams, the north and south Gwash. In May, June and July 1977, Harper (op. cit.) observed differences in chlorophyll-a concentrations and in the temporal sequences of algal species between the two arms and the central basin. He suggested that the reservoir may be considered as three units for management and that the dominant factors affecting algal distribution are the location of nutrient input and wind action.

c) Discussion

No substantial evidence is available concerning the source of algal colonisers for Rutland Water. In 1975 the only water present in the reservoir was derived from the natural catchment; thus it is likely that the majority of algal species recorded in that year were derived from the River Gwash. Other possible routes for invading algae and other organisms are shown in Figure 23.

As algae are non-motile they must rely on passive methods of dispersal to enable them to colonise new habitats. This transfer may be effected by wind, carrying air-borne algae (Gislen, 1948) or transport by animals, for example wildfowl, attached to feet and feathers (Gislen, op. cit.), or after passage through the gut (Atkinson, 1980). Other animals, including man, may also transport viable organisms from one site to another.

As would be predicted from the data on the water chemistry of the reservoir, large algal populations and species compositions similar to other eutrophic reservoirs were observed. Chlorophyll-a concentrations (50 mg m^{-3}) and gross primary production ($300\text{--}500 \text{ mg C m}^{-2} \text{ day}^{-1}$) are also typical of a eutrophic reservoir (Harper, pers. comm.).

In spring 1975 the chlorophyll-a concentration in the central basin reached 79 mg m^{-3} (Fig. 22), the highest value recorded throughout the study period. Low concentrations were recorded throughout the summer period, possibly as a result of uptake of

BURLEY FISHPONDS AND
OTHER AQUATIC HABITATS
WITHIN RESERVOIR BASIN

DISPERSAL FROM OTHER
AQUATIC HABITATS

(passively - transport by wind, man, birds)

(actively - aerial insects)

RIVERS NENE AND
WELLAND (PUMPED WATER)

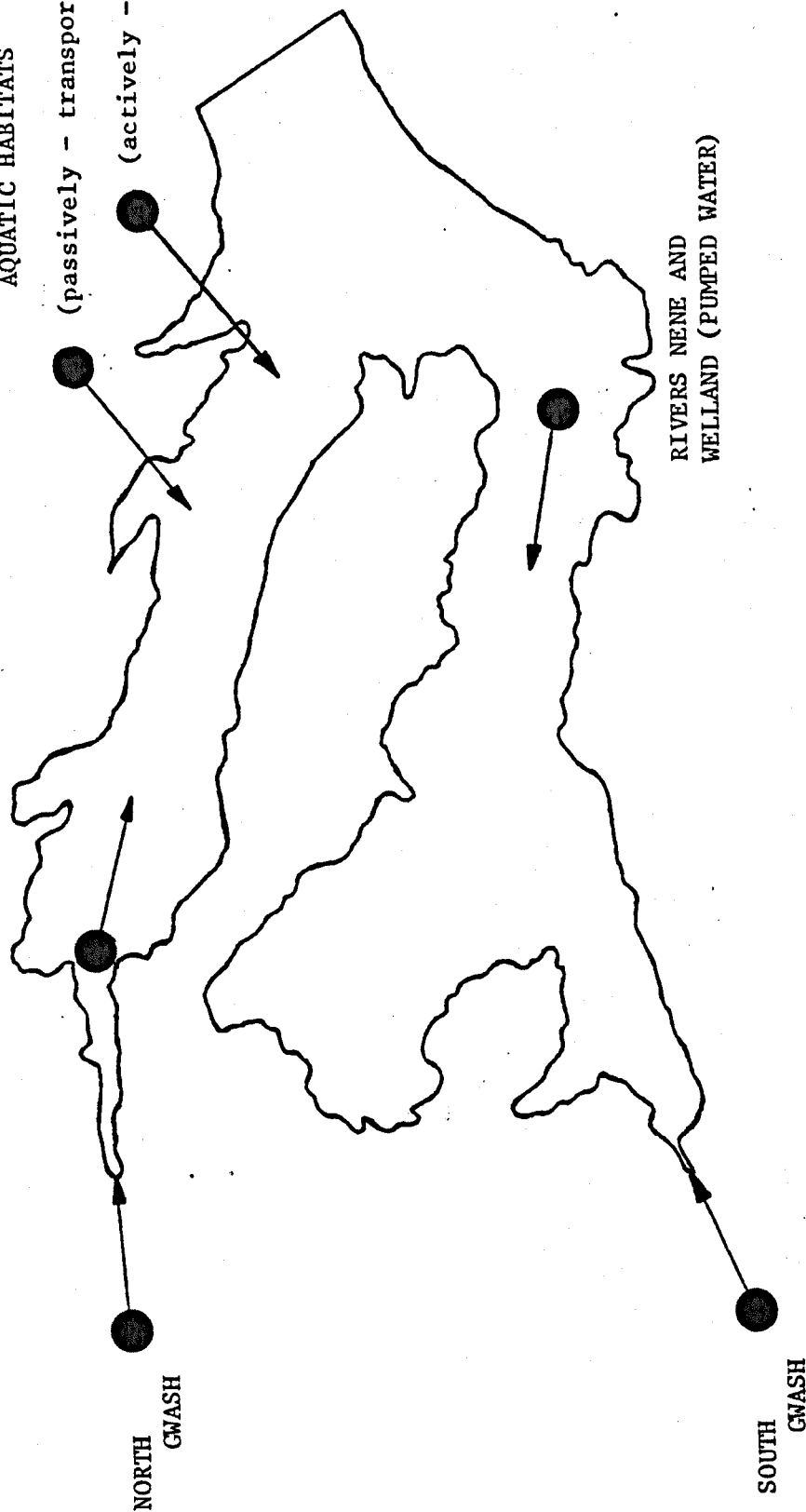


Fig. 23. Possible routes for invading organisms at Rutland Water.

nutrients by algae, particularly Enteromorpha and Cladophora, that were abundant at that time. In 1976 and 1977 approximately 30 species of planktonic algae were recorded (Ferguson, pers. comm.) and seasonal changes in numbers and species were similar to those observed in other lowland impoundments (Toms et al., 1975; Wilson et al., 1978; Youngman, 1975). In 1978 and 1979 approximately 50 species of phytoplankton were recorded in Rutland Water (Ferguson, pers. comm.). The chlorophyll-a concentration was generally lower than in previous years and different species dominated the major algal bloom (Fig.22). These changes may be partly attributable to changes in the water chemistry discussed previously. An idealised diagram of the major seasonal changes and the dominant species of algae that characterise lowland eutrophic reservoirs has been constructed (Fig. 24). From approximately February to April diatoms predominate, from May to August mixed species of green algae predominate and from September to October blue-green algae predominate. As observed at Farmoor reservoir (Youngman, 1975) no two years may be exactly alike in species changes although the scheme does act as a broad generalization and will serve as a basis for discussion of seasonal trends as they relate to other organisms and the management of the reservoir.

Initially (1975 and 1976) the amount of allochthonous organic material in the reservoir was high. This was mainly composed of flooded terrestrial vegetation. As decomposition of the vegetation proceeds so nutrients are released altering the physical and chemical characteristics of the water. Decomposing allochthonous vegetation together with epiphytic, epilithic and epipelagic algae and phytoplankton form the basis of the early grazing food chains in the reservoir. It is only after a period of time that autochthonous material begins to play an important role in the reservoir (McLachlan, 1977). Phytoplankton are the main primary producers in new reservoirs and are the most important energy source for secondary production. The relationship between the phytoplankton and the invertebrate fauna is discussed in Chapter 5.

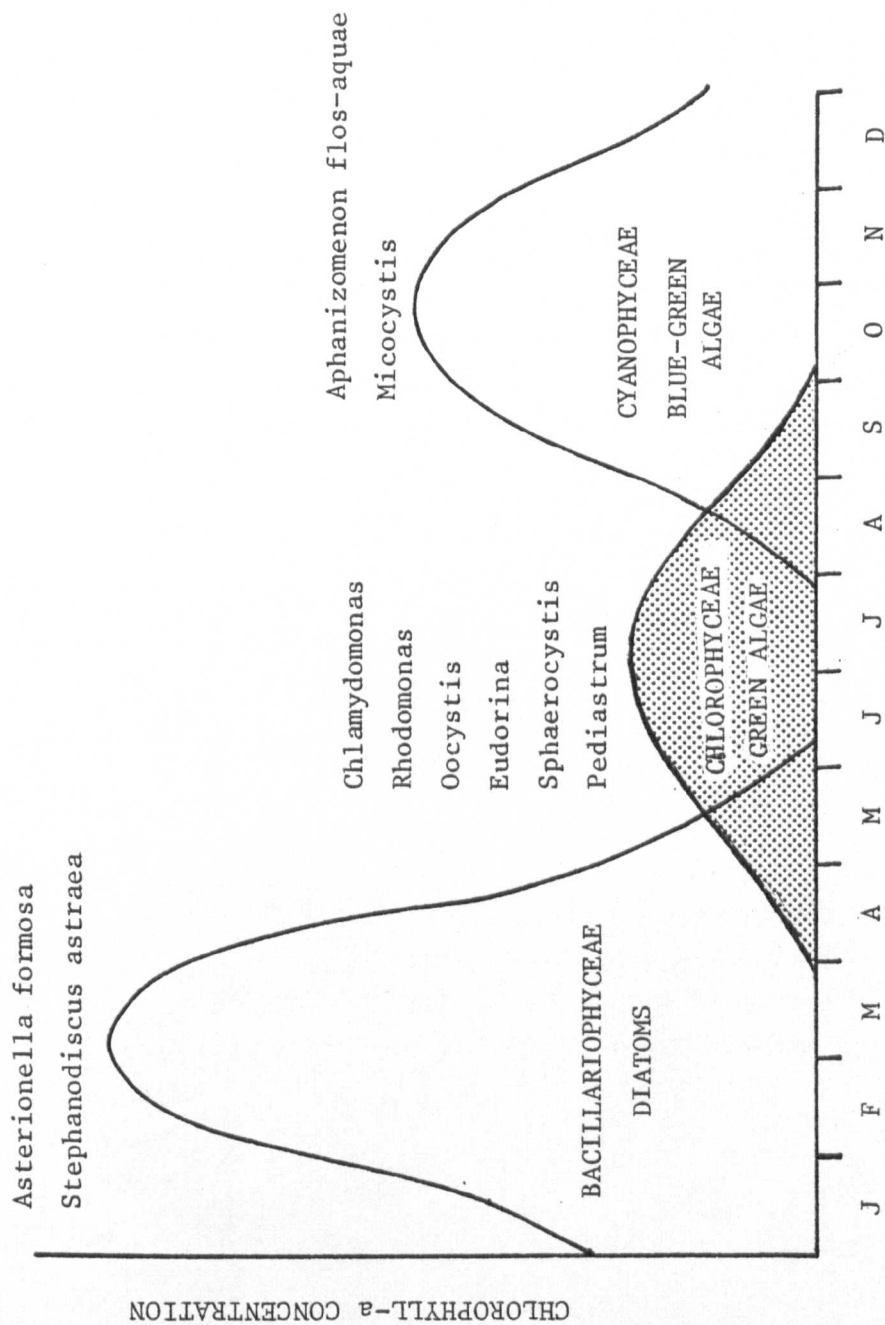


Fig. 24. Schematic diagram of the major seasonal changes and some characteristic species that occur in a eutrophic reservoir. (based on Toms et al, Youngman, Harper)

Invertebrates (excluding Chironomidae)

Research on the benthic macro-invertebrate fauna of Rutland Water began in 1972 after the formation of the Rutland Water Research Committee. Bullock and collaborators (pers. comm.) investigated the fauna of the River Gwash before impoundment and, later, the development of benthic invertebrate populations within the reservoir, utilising artificial substrates, grab and dredge samples. Particular attention was paid to the ecology of Asellus spp. and the production and ecology of leeches. Early work on the possible sites from which benthic invertebrates could colonise the reservoir was conducted by Morton (pers. comm.). For the present study chironomid larvae, obtained from the collections made by Bullock and Morton, were examined and the relevant data presented in Chapter 5.

a) Invertebrate fauna of the reservoir

An invertebrate species list (Table 12) has been compiled with the help of Bullock, Gibson and Warlow (pers. comm.). The choice of sampling methods, principally grab samplers, probably results in an under-representation of some groups (e.g. Corixidae, Dytiscidae, Baetidae) and over-representation of others (e.g. Oligochaeta). Certain taxonomic groups such as the Rotifera and Nematoda have not been identified to species. Consequently this section is intended to provide a general view of the invertebrate fauna and is not an exhaustive account.

A total of 71 taxa (excluding the Chironomidae) has been recorded. Several species have been excluded either due to doubtful identification or because they are considered to be

Table 12: Invertebrate species list for Rutland Water and scale of abundance. 0 - insufficient data; 1 - single record; 2 - rare, occasional, or in small numbers; 3 - regular though not abundant; 4 - abundant and regular; 5 - changing abundance.

	Abundance Scale	Notes
PORIFERA		
Spongillidae	2	Recorded on submerged twigs
COELENTERATA		
Hydra sp.	5	Summer 1977 very abundant
PLATYHELMINTHES		
Polycelis nigra (Muller)	4	All abundant but patchy distribution
Dugesia lugubris (Schmidt)	4	
Dendrocoelum lacteum (Muller)	4	
ROTIFERA	4	
NEMATODA	2	
MOLLUSCA		
Hydrobia sp.	0	Very abundant 1977
Potamopyrgus jenkinsi (Smith)	5	
Bithynia tentaculata (L.)	2	Abundant throughout
Lymnaea peregra (Muller)	4	
Physa fontinalis (L.)	5	
Planorbis albus Muller	2	
Planorbis planorbis (L.)	0	
BIVALVIA		
Sphaerium sp.	2	
Pisidium sp.	2	
OLIGOCHAETA		
Ophidonais serpentina (Muller)	0	Only recorded in Nene Large populations in summer 1977
Nais elinguis Muller	4	
Nais pardalis (Piguet)	0	
Stylaria lacustris (L.)	5	
Tubifex tubifex (Muller)	4	
Psammoryctes barbata (Grube)	0	
Potamothrix hammoniensis (Michaelson)	0	

Table 12: continued

Enchytraeidae	0	
Haplotaxis gardioides (Hartmann)	0	
Lumbriculus variegatus (Muller)	5	Abundant late 1978
HIRUDINEA		
Piscicola geometra (L.)	4	
Theromyzon tessulatum (Muller)	2	
Hemiclepsis marginata (Muller)	2	Abundant October 1977
Glossiphonia complanata (L.)	3	
Helobdella stagnalis (L.)	4	Most abundant leech
Erpobdella octoculata (L.)	4	
HYDRACARINA		
CLADOCERA		
Daphnia hyalina Leydig	0	
Daphnia magna Straus	0	
Daphnia pulex (De Geer)	0	
Chydorus sp.	0	
Eurycercus lamellatus Muller	0	
OSTRACODA		
Cypris sp.	0	
COPEPODA		
Diaptomus sp.	0	
Cyclops sp.	0	
MALACOSTRACA		
Asellus aquaticus (L.)	4	Competes with A.meridianus
Asellus meridianus Racovitza	5	
Gammarus pulex (L.)	4	
EPHEMEROPTERA		
Cloeon dipterum (L.)	5	
Caenis horaria (L.)	5	Abundant dam area 1979
ODONATA		
Platycnemis pennipes (Pallas)	2	
HEMIPTERA		
Gerris sp.	2	
Notonecta sp.	2	
Callicorixa praeusta (Fieber)	0	
Sigara dorsalis (Leach)	0	

Table 12: continued

<i>Sigara ?distincta</i> (Fieber)	0	
<i>Sigara falleni</i> (Fieber)	0	
<i>Sigara ?fallenoidea</i> (Hungerford)	0	
<i>Sigara ?scotti</i> (Fieber)	0	
<i>Sigara concinna</i> (Fieber)	0	
COLEOPTERA		
<i>Deronectes latus</i> (Stephens)	2	
<i>Deronectes depressus</i> (Fabricius)	2	
<i>Agabus</i> sp.	2	Recorded as larvae only
<i>Helophorus dorsalis</i> (Marshall)	2	Only recorded in north-arm
<i>Elmis aenea</i> (Muller)	2	Recorded south-arm 1976
MEGALOPTERA		
<i>Sialis fuliginosa</i> Pictet	2	
TRICHOPTERA		
<i>Agraylea multipunctata</i> Curtis	5	Abundant in 1979
<i>Phryganea grandis</i> L.	2	
<i>Limnephilus lanatus</i> Curtis	5	
<i>Limnephilus ignavus</i> McLachlan	5	<i>Limnephilus</i> spp. abundant dam 1979
<i>Mystacides nigra</i> (L.)	2	
<i>Triaenodes bicolor</i> (Curtis)	2	
<i>Oecetis ?lacustris</i> (Pictet)	2	
DIPTERA		
<i>Tipula</i> sp.	2	Number recorded after water rise
<i>Chaoborus</i> sp.	1	
Ceratopogonidae	2	
Chironomidae	4	See sections Chapter 5

isolated introductions. A single specimen of Niphargus is included in the latter category as this is thought to have originated from one of the deep wells located in the flooded valley floor.

b) Changes in macroinvertebrates

Quantitative data on changes in macroinvertebrate populations (Appendix B) from the time of inundation are available from the transects located at the ends of the north- and south-arms of the reservoir (for locations see Fig. 16). Both of these transects were inundated during the rapid filling of the reservoir between September 1976 and April 1977 (Fig. 9). Sampling began immediately after this rise in water level and continued throughout a relatively stable water level period, April 1977 to April 1979.

The first samples collected in May 1977 contained a few terrestrial invertebrates, particularly oligochaetes and tipulid larvae (Tables 13 and 14). These organisms continued to be found in samples for 3 months, until August 1977. Terrestrial oligochaetes were again found in samples from both transects after an increase in water level in July 1978 (Tables 13 and 14, Fig. 9).

Taxa showing rapid population growth and decline

During the early filling phase several aquatic taxa showed explosive population growth with a subsequent rapid decline. Hydra were ^{first} recorded in large numbers in the south-arm transect in June 1977 (Table 13) and a month later in the north-arm transect (Table 14). This group was recorded on a number of subsequent occasions but in comparatively small numbers. Triclad s were not recorded until 1978 but an unusually large population was recorded in July 1978 in the north-arm transect (Table 14). The largest numbers were recorded near the centre of the transect at 4.5 m and 6.5 m depth. The population

	12. 5 77	26. 5. 77	20. 6. 77	11. 7. 77	31. 8. 77	26. 9. 77	24. 10. 77	29. 11. 77	16. 1. 78	28. 2. 78	16. 3. 78	12. 4. 78	17. 5. 78	13. 6. 78	10. 7. 78	17. 8. 78	19. 9. 78	23. 10. 78	20. 11. 78	14. 12. 78	25. 1. 79	19. 3. 79	19. 4. 79	
Hydra			3	83																				
Tricladida											6	12												
Mollusca										3														
Oligochaeta	29	106	467	870	598	406	77	80	48	19	128	77	3	3	29	381	192	493	1133	99	182	490	243	486
Aquatic																								
Terrestrial	6	3	13													6								
Hirudinea			6			6					3	16		6		19	13	16	22	42	10	6	29	
Asellus			80				13	451	6	64	714	749	170	61	45	262	429	291	93	195	118	48	77	
Gammarus						10			22	179	16	32	6	70	118	611	243	454	239	368	291	144	234	
Ephemeroptera							3																	
Hemiptera			3																					
Coleoptera			3																					
Larvae																								
Adult																								
Trichoptera.																								
Tipulidae	6		13						9															
Ceratopogonidae			3			6																		

Table 13: Changes in macroinvertebrate populations in the second south-arm transect.
Means (m^2) based on ten grab samples.

	12. 5. 77	26. 5. 77	20. 6. 77	11. 7. 77	31. 8. 77	26. 9. 77	24. 10. 77	29. 11. 77	16. 1. 78	28. 2. 78	16. 3. 78	12. 4. 78	17. 5. 78	13. 6. 78	10. 7. 78	17. 8. 78	19. 9. 78	23. 10. 78	20. 11. 78	14. 12. 78	25. 1. 79	19. 3. 79	19. 4. 79
Hydra				10														10				30	54
Tricladida												6			96								
Mollusca					3	22						3			16	28	22	45	30	3	10	6	19
Oligochaeta	115	45	605	1901	374	502	109	80	27	29	38	6	3	3	202	22	26	602	1120	192	61	128	333
Terrestrial	10		6	3											13								
Hirudinea		3	38	3		6		3				3	3	3	35	58	61	166	102	38	22	51	30
Asellus			285		13	205	221	61	538	390	99	608	314	236	3171	1997	1184	7402	1533	2627	477	1171	323
Gammarus	35			3	3	189	378	29	45	262	67	77	38	41	160	413	732	2259	701	509	288	432	390
Ephemeroptera					3	10											10	6					
Hemiptera			3		6	35												12					
Coleoptera Larvae																3							
Adult																	3						
Trichoptera										6		3						70	224	83	3	10	3
Tipulidae	3	6	3					44	26	16			3										
Ceratopogonidae			3	3	3	3	3	3			3												

Table 14: Changes in macroinvertebrate populations in the second north-arm transect.
Means (m^{-2}) based on ten grab samples.

fluctuations recorded throughout the study period for this group may be attributable to a highly clumped distribution along the transect line. Visual evidence for this was obtained during a sub-aqua dive along the transect line. Sampling error due to disturbance of the surface sediments may also contribute to the fluctuations.

During June and July 1977 large populations of the oligochaete Stylaria lacustris developed. Maximum population densities were recorded in the north-arm in July ($1,901 \text{ m}^{-2}$) and in the same month in the south-arm (870 m^{-2}) (Tables 13, 14 and Fig. 25). The numbers declined throughout the winter period. Several oligochaete species were recorded in 1978 and populations fluctuated in both arms of the reservoir. A peak in numbers was recorded in July in both arms and the dominant species was S. lacustris. A second peak in numbers for 1978 was recorded in October in the south-arm and in November in the north-arm; the dominant species was Lumbriculus variegatus (Fig. 25).

Numerically dominant taxa

Several invertebrate groups although recorded intermittently during 1977 were recorded regularly during 1978. Molluscs, dominated by Lymnaea peregra, were recorded regularly in the south-arm from May (Table 13) and in the north-arm from July (Table 14). Hirudinea were recorded in larger numbers in the north-arm than in the south-arm during 1977 and 1978 (Tables 13 and 14). The numerically dominant species recorded was Helobdella stagnalis. In both arms of the reservoir catches of the Malacostraca outnumbered those of other taxa (Tables 13 and 14). Large populations of Asellus spp. were recorded in the north-arm in late 1978 (Fig. 26). The population densities were an order of magnitude greater than those recorded in the south-arm over the same period. The largest populations were associated with partially decayed filamentous algae after the summer growth. These deposits of organic material did not occur

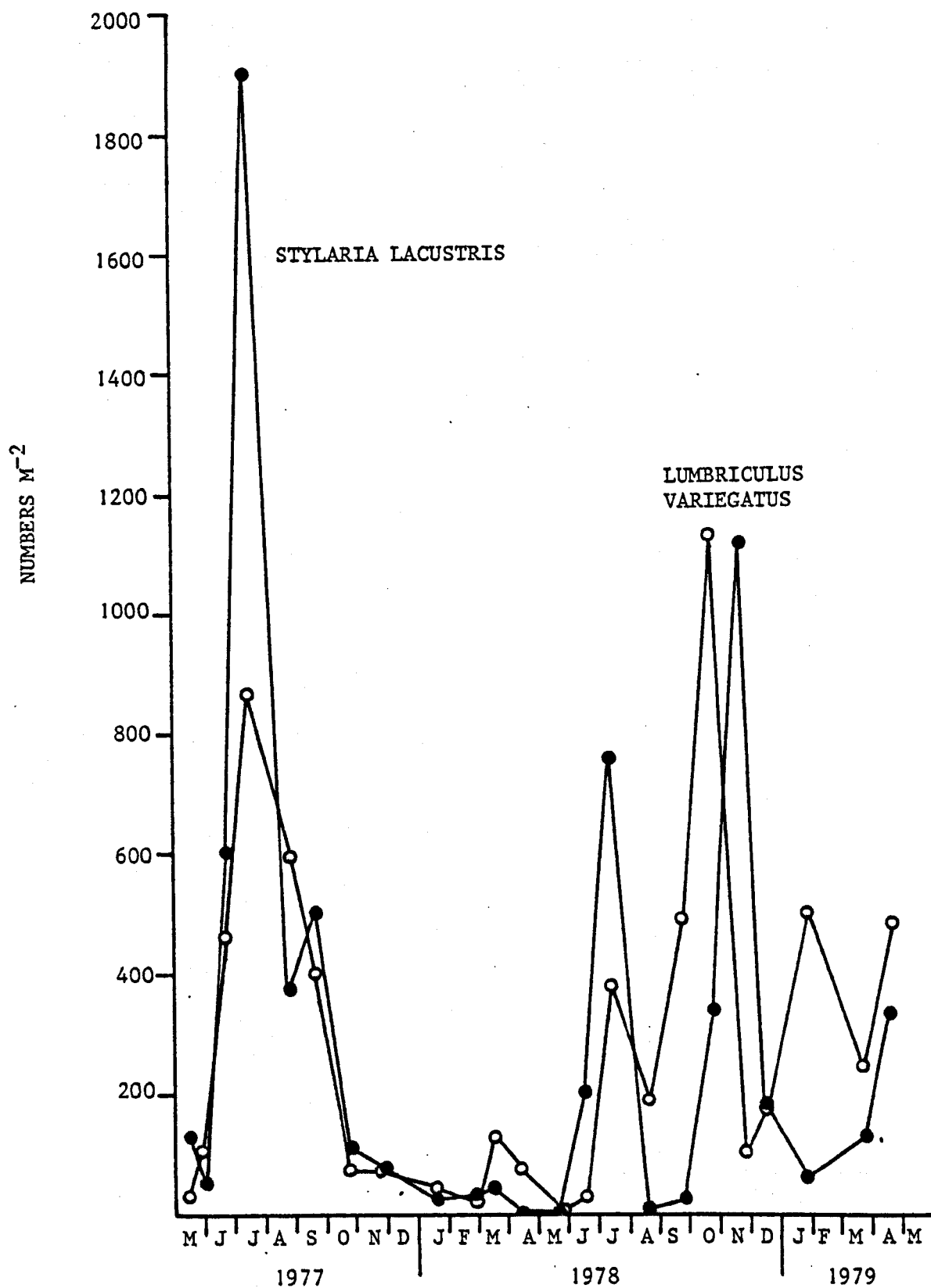


Fig. 25. Changes in the abundance of oligochaetes, mean of ten grab samples. ● second north-arm transect; ○ second south-arm transect. The numerically dominant species are indicated.

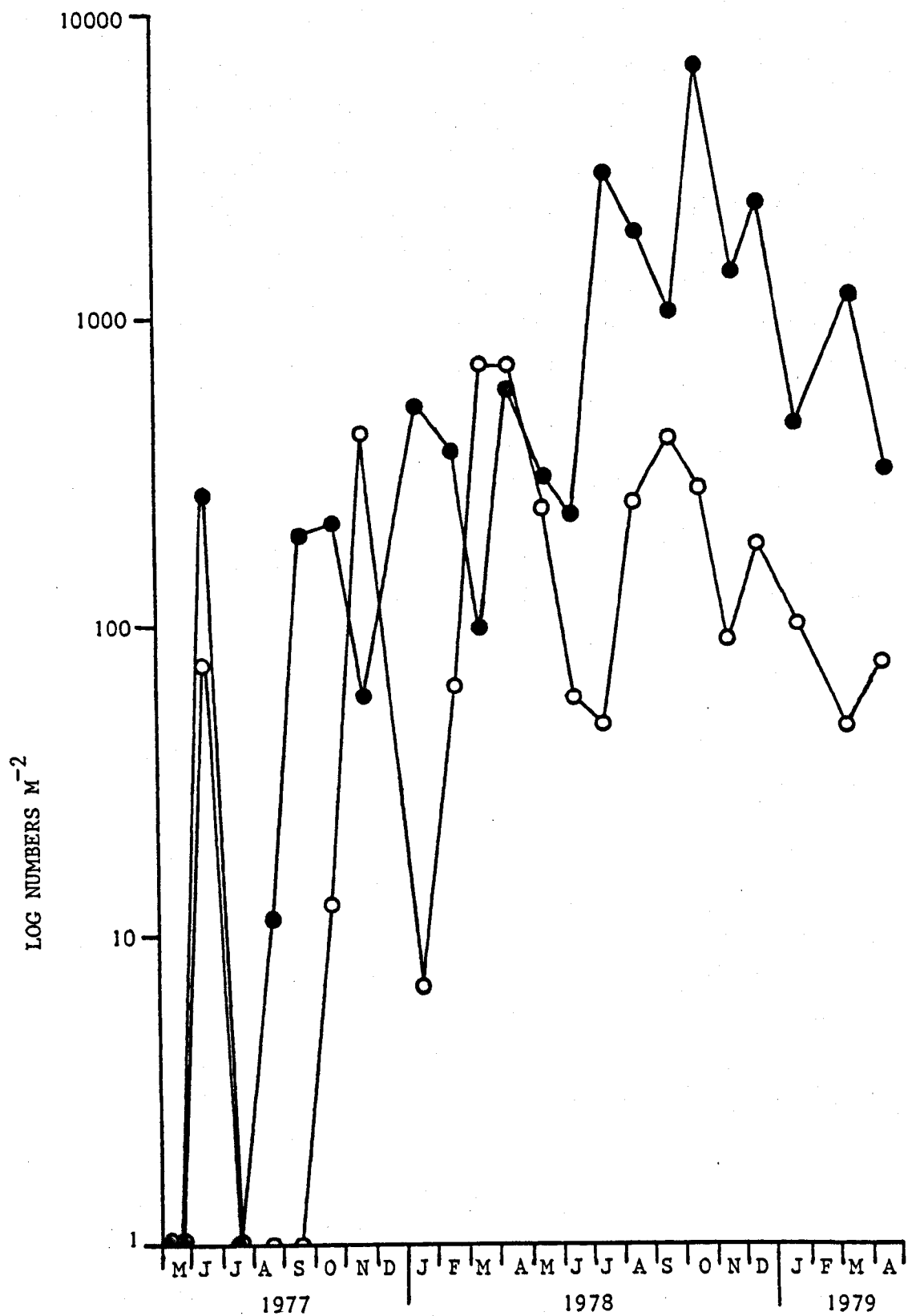


Fig. 26. Changes in the abundance of Asellus, mean of ten grab samples. ● second north-arm transect; ○ second south-arm transect.

to the same extent in the south-arm due to the steeply shelving shore and the effects of wave erosion.

The distribution of Asellus across each transect on each sampling date is shown in Figure 27. Until July 1978 high population densities were only found near the centre of the transect in the vicinity of the old stream bed. Underwater diving observations confirmed the presence of rich organic sediments in the old stream bed whilst the rest of the area was composed of undecayed terrestrial vegetation. During the remainder of 1978 the observed population density of Asellus increased towards the ends of the transects. This redistribution of Asellus was not so pronounced in the south-arm probably because there was less organic material available in the marginal zones. The largest populations recorded in August, September and October in the south-arm occurred on the leeward side of the transect where some growth of filamentous algae occurred.

Gammarus pulex was recorded from both arms of the reservoir. Observed population densities increased from less than 50 m^{-2} in May 1978 to a maximum of 610 m^{-2} in August in the south-arm transect and to a maximum of $2,259 \text{ m}^{-2}$ in October 1978 in the north-arm transect (Fig. 28). Although G. pulex is also usually associated with decaying organic matter, a more even distribution along each transect was observed compared to Asellus (Fig. 29). This may be attributable to its greater mobility and broader niche requirements. The greater mobility of Gammarus may also lead to avoidance of the grab sampler, resulting in a higher degree of sampling error.

Taxa showing slow population growth

Ephemeroptera, Hemiptera, Coleoptera and Trichoptera were all recorded occasionally and in low numbers from both transects (Tables 13 and 14). This appears to be partially due to slow colonisation of the reservoir and to the unsuitability of a grab sampler for quantitative estimates of these actively moving groups.

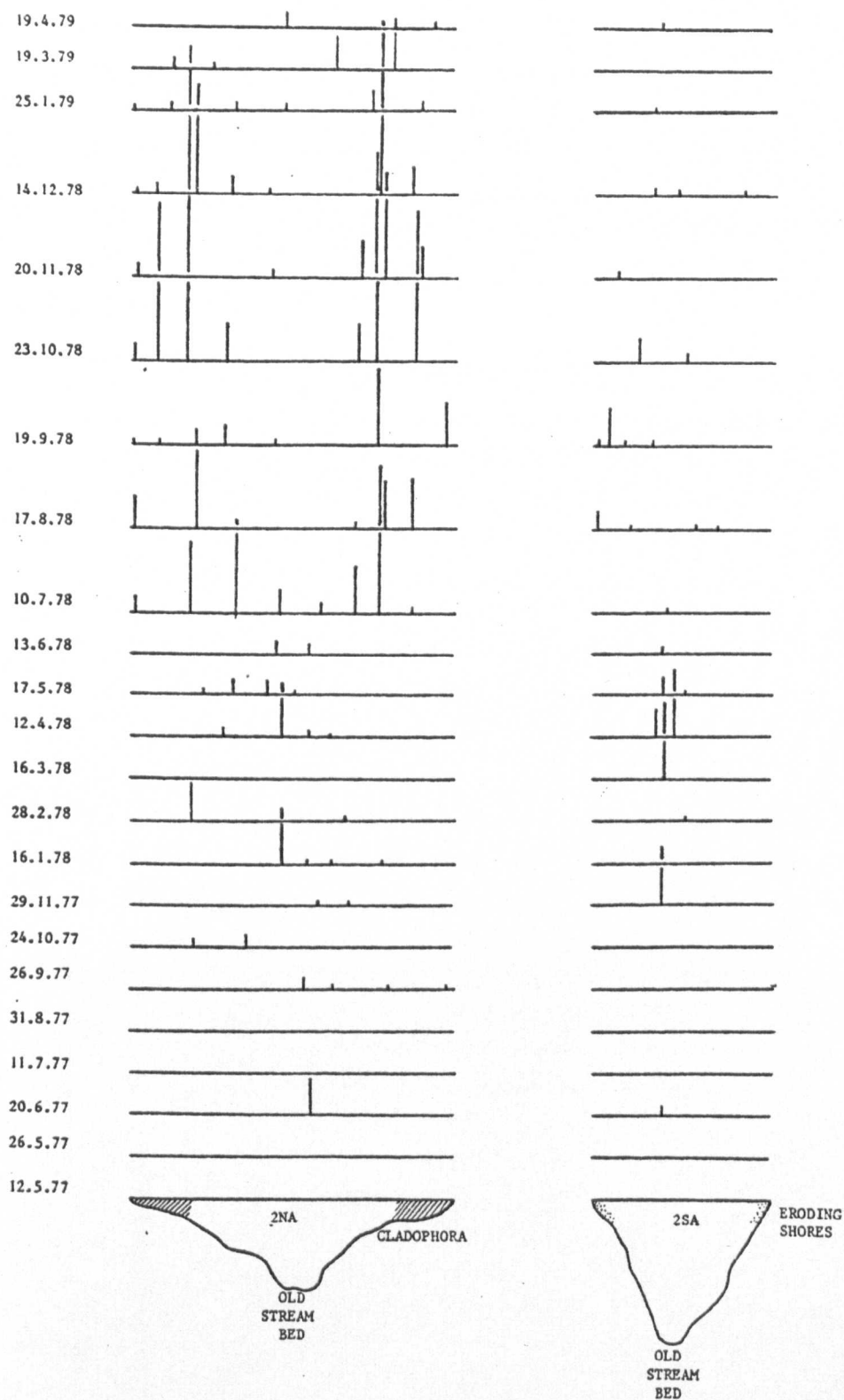


Fig. 27. Changes in the numbers and distribution of *Asellus* across the second north-arm and south-arm transects.

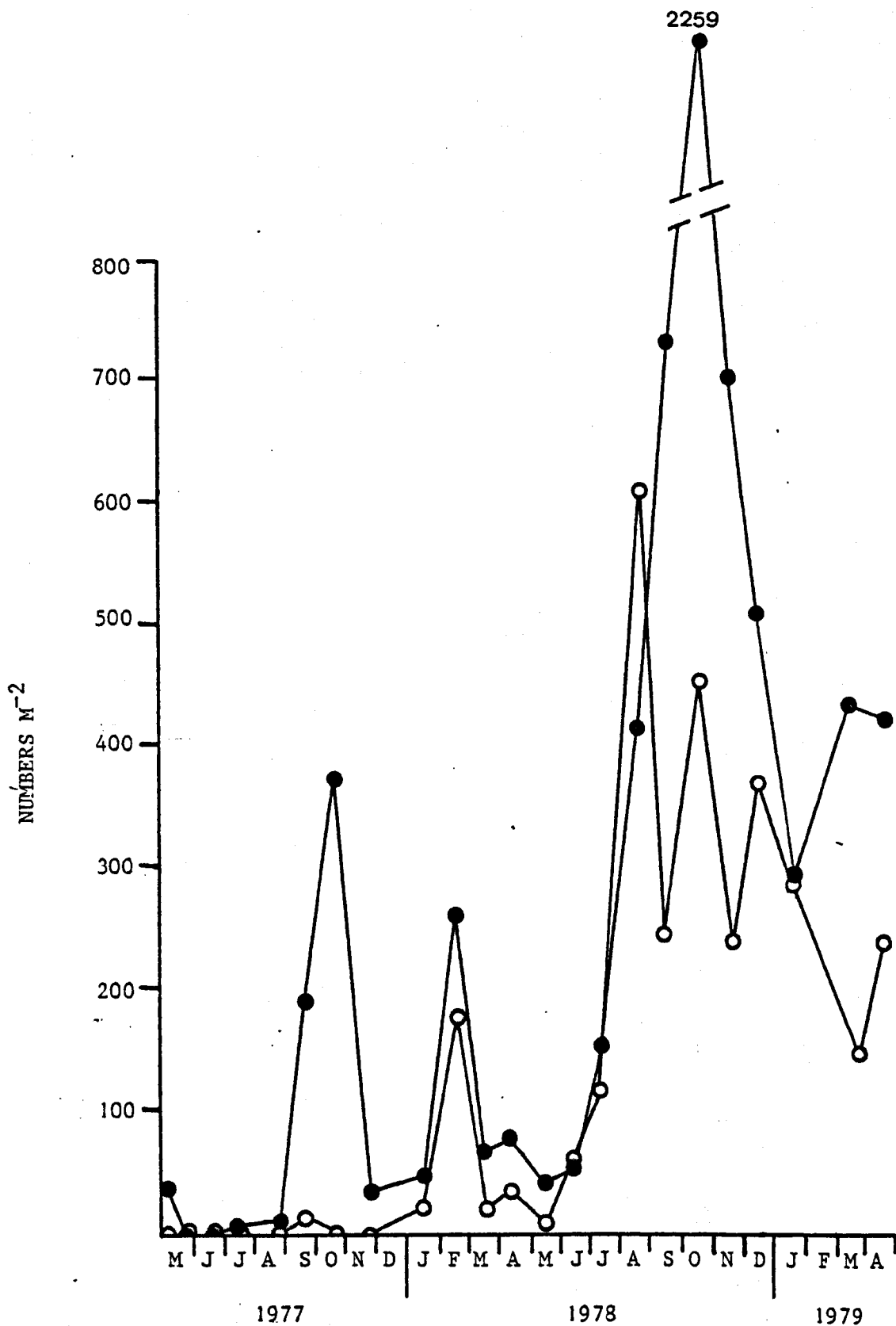


Fig. 28. Changes in the abundance of *Gammarus*, mean of ten grab samples. ● second north-arm transect; ○ second south-arm transect.

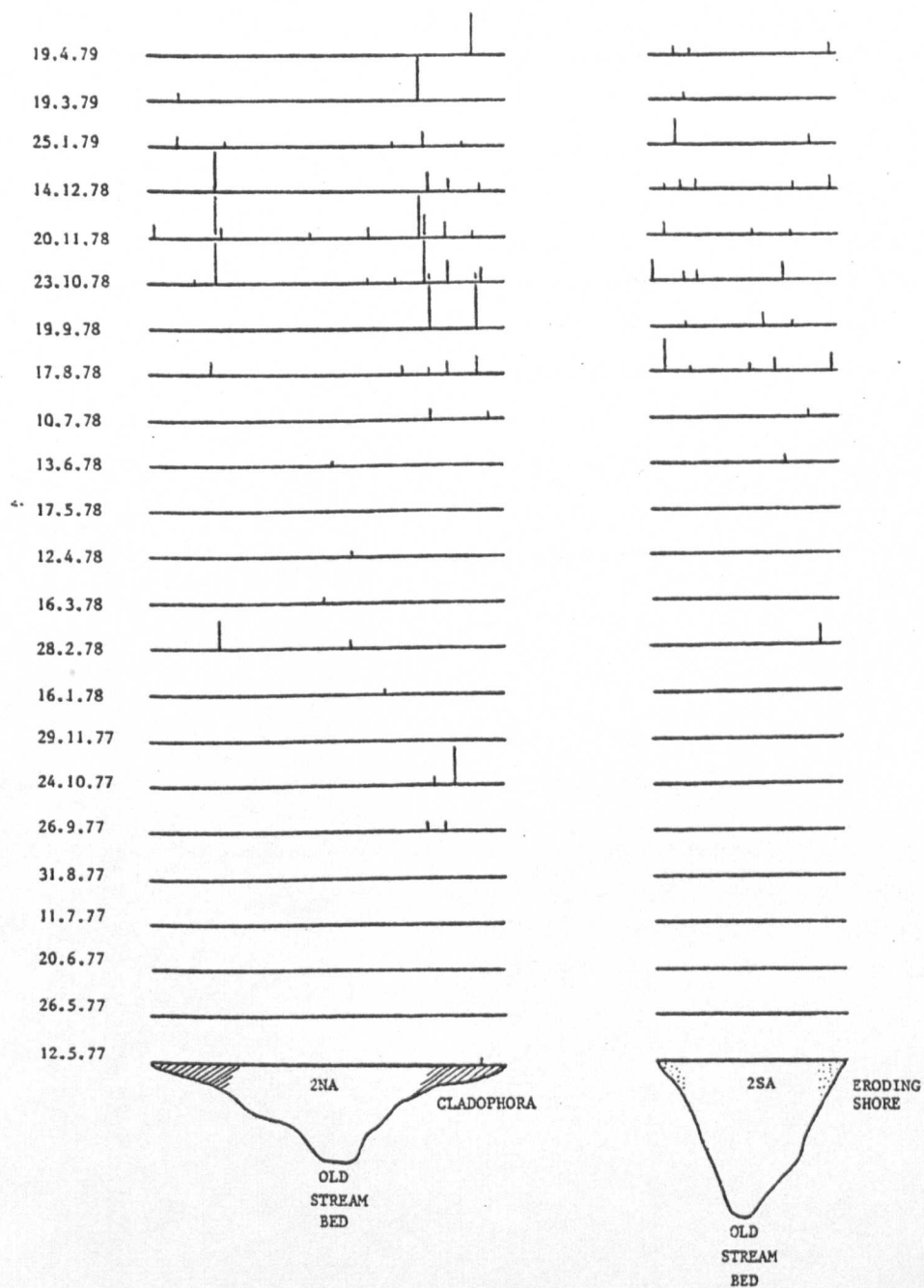


Fig. 29. Changes in the numbers and distribution of *Gammarus* across the second north-arm and south-arm transects.

c) Discussion

Inundation of grassland

Benthic invertebrate samples, collected in May 1977, on vegetation that had been flooded for a period of approximately two months, revealed large numbers of terrestrial invertebrates and no aquatic invertebrates. The abundance of these terrestrial organisms is likely to have been underestimated in the grab samples due to their apparent accumulation at the invading water's edge. Arachnids, thrips and earthworms were found by Campbell (1963) in the newly flooded vegetation at Loch Garry and similar observations at other new reservoirs have been recorded by Sokolova (1963), Paterson and Fernando (1969), Krizanck (1970) and Armitage (1977).

A number of workers have commented on the importance of terrestrial organisms, particularly earthworms, in the diet of fish in newly flooded areas of lakes and reservoirs (Runnestrom, 1955; Campbell, 1963; Kennedy and Fitzmaurice, 1971; Crisp, Mann and McCormack, 1978). The major invertebrates found in temperate grassland, such as that inundated by Rutland Water, are indicated in Table 15. The more important organisms in fish diet are likely to be the larger organisms such as Mollusca, Coleoptera and Diptera larvae, Lumbricidae and Arachnida.

Macfadyen (1963) estimated the biomass of invertebrate organisms in a meadow grassland to be 189.5 g m^{-2} , and in a limestone grassland 191.1 g m^{-2} . In some base rich grasslands earthworm biomass alone may exceed 100 g m^{-2} (Wallwork, 1970). Using the figure for a meadow grassland provided by Macfadyen (1963) approximately $2.4 \times 10^6 \text{ kg}$ of terrestrial invertebrates were inundated by Rutland Water. Not all of this enormous biomass will be available as fish food as many of the organisms may die underground. However, a study by Roots (1956) on the effects of flooding on British earthworm species revealed that some species could survive immersion for 8 to 12 months and

Table 15: Major groups of invertebrates found in soil in a cool temperate grassland (based on a figure in Kevan, 1965)

	Thousands m ⁻²	
	Max.	Min.
NEMATODA	120 ⁶	1.8 ⁶
ENCHYTRAEIDAE	20	0.3
LUMBRICUS	1.3	0.2
MOLLUSCA	7	0.2
MYRIAPODA	2	1
ISOPODA	0.5	0.2
FORMICOIDEA	0.7	0.5
COLEOPTERA LARVAE	1	0.5
DIPTERA LARVAE	1	0.9
ARACHNIDA	0.8	0.3
COLLEMBOLA	40	10
ACARINA	120	20

that their behaviour would make them available to fish. Campbell (1963) estimated that earthworms would be present up to 18 months after flooding terrestrial vegetation at Loch Garry. At Rutland Water earthworms were found in trout stomachs from November 1976 to August 1977, a period of 10 months. The last earthworms were found in stomachs only 4 months after the reservoir was full (Warlow, pers. comm.).

Invasion by aquatic invertebrates

The creation of a new habitat, such as a new reservoir, provides organisms with the opportunity to exploit its resources. However, few data are available on how aquatic invertebrates disperse from one water body to another.

Organisms in a uniform environment may radiate out in all directions and those that come by chance into a suitable habitat may become established. The mechanism is not entirely random as other agents of dispersal, for example wind and water currents, may channel the organisms in restricted directions. Organisms may also exhibit tropisms in relation to various environmental factors which influence their direction of movement. Aquatic insects with aerial adult stages may disperse by active flight.

Heape (1931) introduced the term passive dispersal for those organisms that are carried to new habitats by agents, for example wind, animals, man. Gislen (1948) suggested that small organisms may be carried on birds' feet and feathers. Bondesen and Kaiser (1949) believed that the snail Potamopyrgus jenkinsi may be eaten by birds and later regurgitated. The importance of man, particularly fishermen and naturalists, in transporting aquatic organisms is stressed by Moon (1957a and b).

At Rutland Water a number of surrounding aquatic habitats may be the source of invading organisms and a variety of routes and mechanisms employed (Fig. 23). The earliest aquatic

invertebrate species recorded in the reservoir are likely to have been derived from the River Gwash as this was the only direct inflow of water to the reservoir in 1975. These organisms may have occurred within the river during inundation or have been carried into the reservoir in the drift. However, Dendy (1944) showed that drifting stream organisms carried into a lake did not survive for long. As the River Gwash is composed of both riffles and pools it is likely that silty substrates will occur which will contain organisms able to survive lentic conditions. Few quantitative data are available for Rutland Water on the first invading species. Samples obtained a few months after closing the dam indicate that the Chironomidae were the numerically dominant group. These may have been derived either from the River Gwash or by active dispersal of aerial adults from other aquatic habitats.

Colonisation by benthic invertebrates

Paterson and Fernando (1969) divided the species present in a lotic community into two groups on the basis of their ability to colonise a reservoir. The first group is composed of those species unable to reproduce in the new lentic habitat whilst the second group is composed of those species able to survive and reproduce in the new lentic conditions.

The first group includes organisms such as Simulium and Hydropsyche larvae (Paterson and Fernando, 1969) that are unable to survive in the new habitat as they are highly adapted to living in flowing water. Also included in the first group are organisms such as Limnephilus, Orthocladius and Metriocnemus larvae. These may survive in the new habitat to complete the life cycle but the adults are unable to reproduce successfully. This may be due to the absence of sites for oviposition or ^{of} chemical and physical cues for oviposition.

The second group of organisms (described by Paterson and Fernando, 1969) included species of oligochaete, nematode,

corixid and chironomid that are all able to survive and reproduce in the new habitat. These species are preadapted to conditions in a lentic habitat.

At Rutland Water a number of species present in the River Gwash were not recorded in reservoir samples, particularly several species of oligochaete, hemipteran, trichopteran and coleopteran. These organisms fit into the first category described by Paterson and Fernando (op. cit.). A number of species that occurred in the River Gwash have been recorded in the reservoir throughout the study period, for example the triclad Dendrocoelum lacteum and several species of oligochaete, leech and hemipteran. These organisms fit into the second category described by Paterson and Fernando (op. cit.). Investigations on this aspect of the reservoir's development are being undertaken by Bullock (pers. comm.) and will not be discussed further here.

Unfortunately at Rutland Water insufficient data are available to estimate the numbers and species of organisms that entered the reservoir via the pumped river water. However, it is interesting to note that for one species of oligochaete, Nais pardalis, the only previous British record was from the River Nene (Brinkhurst, 1971).

The earliest colonising taxa at Rutland Water (Table 16) are r-selected on the continuum of bionomic strategies. Slow colonising species such as the Ephemeroptera are K-selected. This slow colonisation may be due to slow rates of dispersal or to the initial unsuitability of the habitat.

Successional changes in invertebrate populations

A number of workers have observed rapid population growths with equally rapid declines in a wide variety of organisms during the early development of new reservoirs (e.g. Balinsky and James, 1960; Biswas, 1966; Ewer, 1966; Petr 1969). At

Table 16: Relative rates of colonisation of some taxa at
Rutland Water

Taxa with quickly colonising species (r-selected)	Taxa with slowly colonising species (K-selected)
Hydra Tricladida - <u>Dendrocoelum lacteum</u> Oligochaeta - <u>Stylaria lacustris</u> Malacostraca - <u>Asellus</u> spp. - <u>Gammarus pulex</u> Hemiptera - <u>Corixa</u> spp. - <u>Sigara</u> spp.	Ephemeroptera Odonata Coleoptera Mollusca Trichoptera

Rutland Water Hydra and Stylaria lacustris both showed dramatic population growth and decline.

Less dramatic population changes observed at Rutland Water were attributable mainly to changes in the substrate. Gammarus pulex, an early coloniser probably derived from the River Gwash, was found amongst the most recently flooded vegetation. A similar observation was made by Moon (1935) for newly flooded grassland at Lake Windermere. Asellus spp. were slower to move away from the old river bed where large populations were recorded in the deposits of detritus. Detritus accumulated for approximately one year before large populations of Asellus built up.

The first major substrate change to occur at Rutland Water was the development of epiphytic algae on the flooded terrestrial vegetation. This new habitat provides shelter and food for a variety of invertebrate species (Armitage, 1977). Joffe (1961), Paterson and Fernando (1969), Aggus (1971) and Jones and Selgeby (1974) have all recorded high densities of animals amongst flooded vegetation after varying periods of time. Armitage (1977) suggested that the large numbers of leeches and Gammarus pulex recorded at Cow Green reservoir after impoundment may have been due to the presence of a suitable woody substrate, heather shoots, for attachment and protection. Most woody vegetation was cleared at Rutland Water before flooding but large growths of sponge and numerous leeches were observed on one submerged bush during a sub-aqua observation dive.

Fish

a) Trout fishery

Rutland Water has been developed as a trout fishery and with a surface area of 1,260 ha. is probably the largest, man-made, still-water trout fishery in Western Europe. The reservoir has been stocked with both brown trout (Salmo trutta) and rainbow trout (S. gairdneri) and more recently (1980) with brook trout (Salvelinus fontinalis^{Mitchill}). It is managed on a "put and take" basis as there is no natural recruitment. In order to maintain the trout stocks a hatchery has been built at Horn Mill, approximately 2 miles from the reservoir. The hatchery takes water from the North Brook, a tributary of the River Gwash, which is fed by limestone streams. Trout are reared from eggs using brood fish which in future will be taken from the reservoir. Holding tanks, used prior to stocking in the reservoir, are located below the dam (Plate 2) and are fed by reservoir water. These facilities enable an annual stocking figure of 100,000 to be maintained.

The total weight of fish stocked prior to the opening of the fishing season, April 1977, was 3,340 kg, most fish being put in as fry or fingerlings (Table 17). On the opening of the fishing season in 1977, 55% of the fish caught were brown trout and 45% rainbow trout. This is in contrast to the proportion stocked of which 57% were rainbow trout. Three factors are thought to have contributed to the lower numbers of rainbow

Table 17: Trout stocking at Rutland Water (data provided by Anglian Water Authority)

Date	Trout Species	Number	Mean Wt. (g)	Total Wt. (kg)
1975				
March	Brown	54,000	18.2	983
May	Brown	24,000	1.0	24
May	Rainbow	36,600	2.0	73
June	Brown	48,500	1.2	29
June	Rainbow	170,200	2.5	426
August	Rainbow	50,100	15.5	777
September	Brown	34,100	11.0	375
October	Brown	32,100	7.9	254
1976				
March	Brown	7,740	40.0	310
April	Brown	14,000	0.5	7
May	Brown	58,300	0.84	49
May	Rainbow	102,700	1.28	131
1977				
July	Rainbow	3,330	-	-
August	Rainbow	12,200	-	-
October	Rainbow	5,040	-	-
November	Rainbow	57,640	-	-
November	Brown	3,068	-	-
December	Rainbow	403	-	-

trout caught; mortality due to predation by larger fish stocked earlier in the year; mortality due to high summer and low winter temperatures; the effects of parasitism, mainly by the eyeflukes Diplostomum spatheceum and Tylodephys clavata (Moore, pers. comm.).

The angling success during 1977 is indicated by the results shown in Figure 30. Brown trout provided a steady catch throughout the fishing season, with no restocking during the season. Rainbow trout were stocked during the season in response to the declining catch. A summary of the fish stocked and caught during the first two fishing seasons is shown in Table 18.

In 1975 stocked trout increased in weight from less than 100 g early in the year to 200 g for rainbow trout, and 400 g for brown trout, by the end of the year (Fig. 31). In 1976 the increased rate of growth from March to June and again from September to November corresponds with increases in water level (Fig. 9). The rise in water level results in an increased availability of terrestrial food items on which the trout were feeding (Warlow, pers. comm.). The slightly slower growth rate from June to September 1976 may have been the result of high water temperatures inhibiting feeding. From November 1976 to April 1977 growth rate declined due to low water temperatures, minimum 2°C, inhibiting feeding. Fish weights were also affected during this period by spawning of mature fish. Rapid growth was observed from March to August 1977, reflecting the abundance of food in the reservoir.

b) Coarse fish colonisation

An attempt was made to exclude coarse fish populations from the River Gwash and Burley fish ponds prior to inundation. A combination of rotenone, netting and electrofishing techniques was used (Moore, pers. comm.). Fish are prevented from entering the water pumped from the rivers Nene and Welland by rotating band

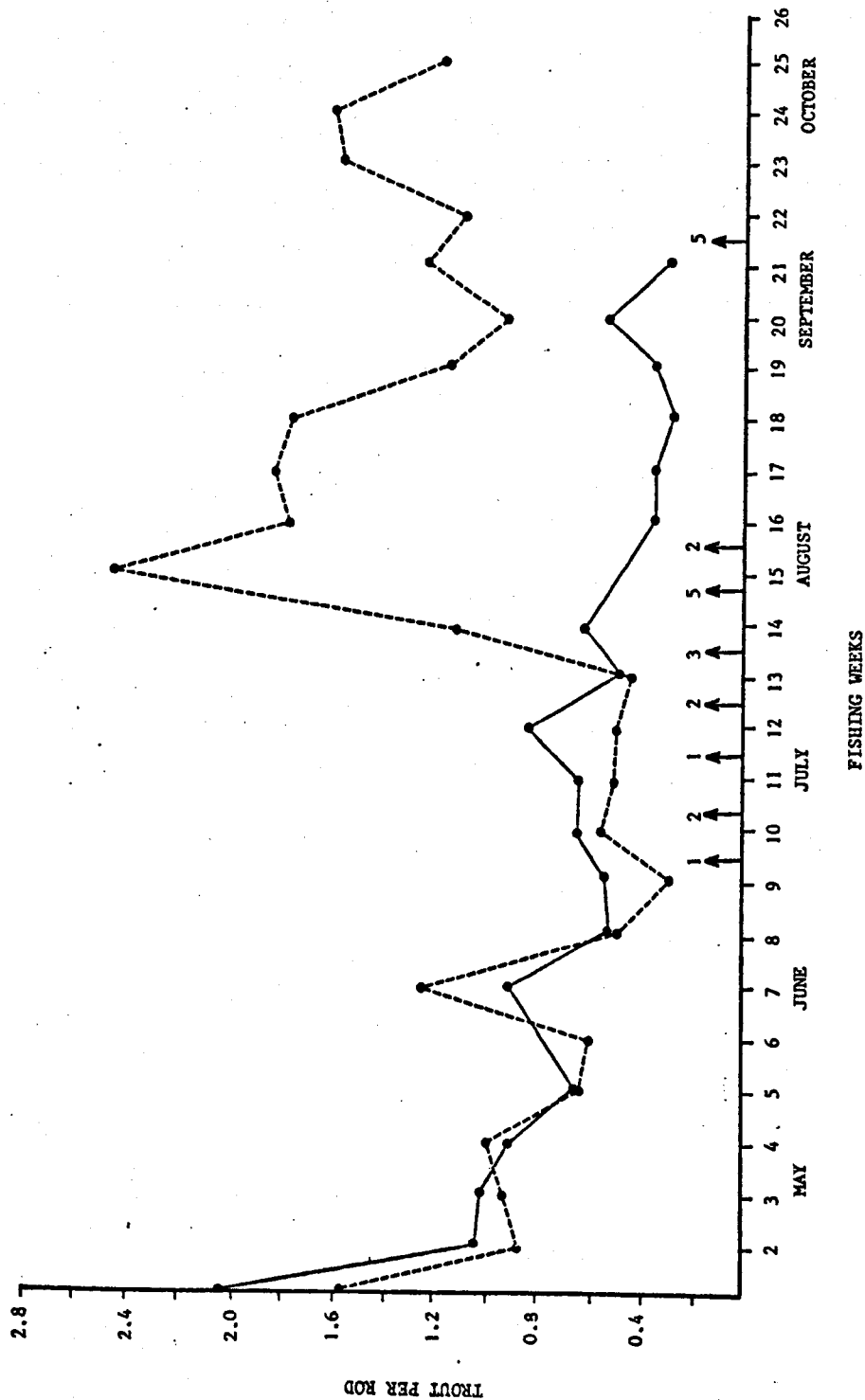


Fig. 30. Fishery success at Rutland Water during 1977. •—• brown trout, —•—• rainbow trout. Number of rainbow trout stocked (thousands) is indicated. (Data provided by A.W.A. and obtained from anglers catch returns).

Table 18: Summary of the fish stocked and caught and some fishery statistics for the first two fishing seasons at Rutland Water (data provided by Anglian Water Authority)

			First fishing season	Second fishing season
	1975	1976	1977	1978
Total fish stocked	449,600	182,740	85,115	54,680
% rainbow	57%	56%	96%	70%
% brown	43%	44%	4%	30%
No. day permits			26,000	34,869
Catch returns received			17,812	26,010
Total fish caught			33,982	69,219
Trout/return			1.9	2.6
Average wt/fish (g)			900	740

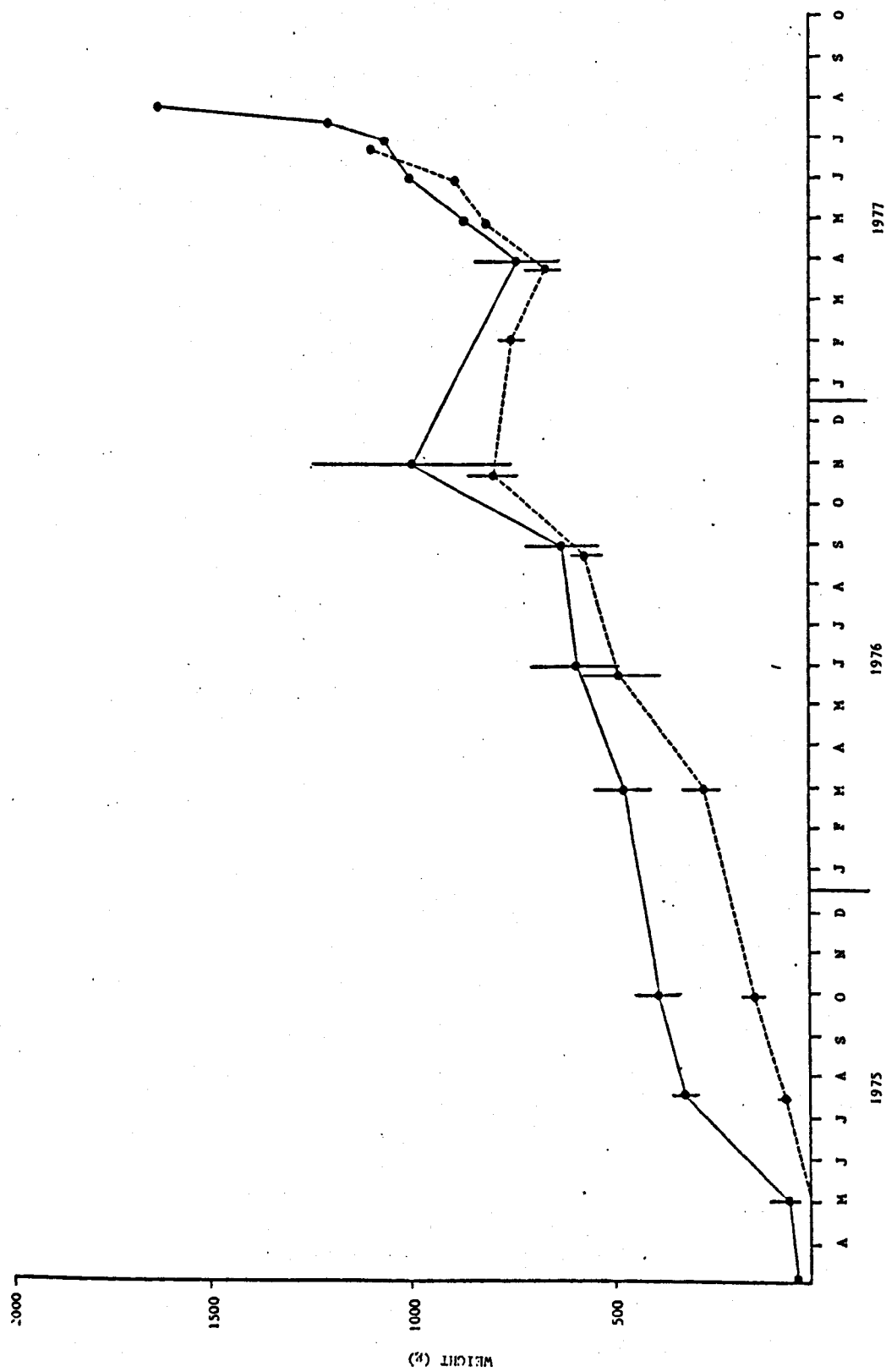


Fig. 31. Growth of rainbow trout and brown trout, 95% confidence intervals are shown. (Data provided by A.W.A.).

screens located at the intakes to the pumping stations. However, fish fry and eggs may pass undamaged through the band screens and enter the reservoir (Moore, pers. comm.). 19 species of coarse fish were recorded in the iver Gwash prior to treatment and inundation and both the rivers Nene and Welland have large populations of coarse fish species (Leeming, 1963; Hart, 1971).

During the first day of the fishing season in 1977 a number of coarse fish were caught by anglers. Estimates for the number of pike (Esox lucius^L) caught vary from 300 to 1,000 (Warlow, pers. comm.). Shoals of coarse fish could also be observed around the reservoir and roach (Rutilus rutilus^(L.)) and stickleback (Gasterosteus aculeatus^L) were particularly common. Coarse fish did not contribute significantly to the diet of trout until 1979 (Warlow, pers. comm.). At this time extensive shoals of coarse fish could be seen in almost all sheltered bays of the reservoir.

c) Discussion

Rutland Water is a eutrophic lowland reservoir that is managed as a trout fishery. Generally in eutrophic lakes and reservoirs populations of salmonids are likely to decline and coarse fish to increase (Larkin and Northcote, 1969). Coarse fish are adapted to the prevailing conditions in a eutrophic water whilst salmonids prefer oligotrophic conditions. At Rutland Water an attempt was made to slow the effects of coarse fish colonisation, by removing existing stocks from all water bodies within the reservoir basin, and to capitalise on the initial high productivity of flooded vegetation by stocking with a high density of small trout.

No quantitative data are available on the effectiveness of removing coarse fish from the iver Gwash but it is thought complete removal of fish is unlikely to have occurred. Thus the River Gwash was probably the source from which early

colonisation of the reservoir by coarse fish took place. It is likely, however, that coarse fish numbers were sufficiently low that predation of trout by pike and competition between other coarse fish species and the stocked trout was negligible, at least during the first two years of the reservoir's existence. By the start of the fishing season in 1977 pike probably increased mortality of the smaller stocked trout.

As no stocked trout were tagged, estimates of their mortality is difficult and can only be based on figures from other trout waters. The 174,000 fish stocked in April and May 1976 had an average weight of 0.8 g and may have suffered heavy mortality from predation by the larger trout introduced in 1975 and from the high summer temperatures in 1976. If we assume for instance a mortality of 60% there were still approximately 200 trout ha⁻¹ at the start of the fishing season in 1977. Crisp and Mann (1977) calculate that an annual stocking rate of 40-60 fish ha⁻¹ in lowland reservoirs managed on a 'put and take' basis will give catches of 20-30 fish ha⁻¹. Thus, although the trout stocked at Rutland Water prior to the start of the fishing season in 1977 were lower in weight than fish at other similar reservoirs, the stocking density was higher.

Eyefluke infections occurred in rainbow trout in 1976 and 1977 and Moodie (pers. comm.) presents some evidence that the majority of fish in the reservoir were uncatchable due to infection. This, in part, may account for the comparatively low numbers of rainbow trout caught during the first fishing season. No infected snails, the secondary host of the eyefluke parasite, have been recovered from the reservoir since June 1977. This suggests that the incidence of infection will decline and make the restocked rainbow trout catchable.

CHAPTER 5
CHIRONOMID ECOLOGY

Introduction

Data on the temporal and spatial variation of the chironomid fauna at Rutland Water are based mainly on collections of larvae. These data have, however, been supplemented by collections of pupal exuviae and adult males. The use of pupal exuviae for determining the relative abundance of chironomid species and the emergence of those species was first suggested by Thienemann(1910). The method has several advantages over methods using other stages of the life cycle. Firstly the exuviae are easily collected and sorted and the time taken in preparation of slides for identification is considerably less than for larvae or adults. Recent advances in the taxonomy of pupae enables their identification to genus and in some cases closely related species show greater morphological variation as pupae than as larvae. The collection of adult males enables species identification but suffers from the disadvantage that adults collected may not have originated within the reservoir.

Data for this chapter have been divided into seven sections. The first section introduces the chironomid fauna of Rutland Water as determined from larval, pupal exuvial and adult samples. For descriptive purposes the population ecology of the family can conveniently be divided into temporal and spatial aspects although there is clearly considerable interaction between the two. Three sections deal with temporal aspects of the chironomid fauna, three sections with spatial aspects and interactions between the two are considered in the final discussion section.

Temporal changes in the abundance of chironomid fauna can be investigated within any chosen time period. Several different levels of measurement are particularly relevant in this study; successional changes, seasonal changes and annual changes. Diel activity of

chironomid larvae and diel emergence patterns were not investigated but are discussed in Chapter 6 in relation to predation by trout. Successional changes are particularly pronounced in a new reservoir such as Rutland Water due to physical and chemical changes in the water and substrate. This has been the subject of several studies (for example, Morduchai-Boltovskoi, 1961; Paterson and Fernando, 1970; McLachlan and McLachlan, 1971). Seasonal changes in chironomid larvae populations are the result of emergence by the aerial adults and this has been investigated by a number of workers (for example, Lundbeck, 1926; Rawson, 1930; Eggleton, 1931; Mundie, 1955; Corbet, 1964). Studies on more mature lakes and reservoirs have recorded year to year fluctuations in faunal composition and numbers (Jonasson, 1961, 1964, 1965, 1972; Charles et al., 1975; Lindegaard and Jonasson, 1979). These annual faunal changes may result from factors such as annual climatic variation.

Spatial aspects of the chironomid fauna have been divided into dispersion patterns, population variations within the reservoir and depth distributions. The formation of a suitable mathematical model to describe the spatial dispersion patterns of larvae permits the use of parametric statistics and enables the errors in population parameters to be estimated. Spatial variation in the chironomid fauna within the reservoir may reflect differences in water quality, an intended design feature, as well as other environmental variables, such as substrate type. The water depth is also an important variable because many other physico-chemical parameters may vary in response to increasing depth.

a) Chironomid fauna of Rutland Water

The family Chironomidae is divided into seven subfamilies (Pinder, 1978) of which three are particularly important in Rutland Water; Tanypodinae, Orthocladiinae and Chironominae. Although species are classified according to taxonomic principles there is generally some ecological basis to the classification. Figure 32 is a simplified pictorial representation of the

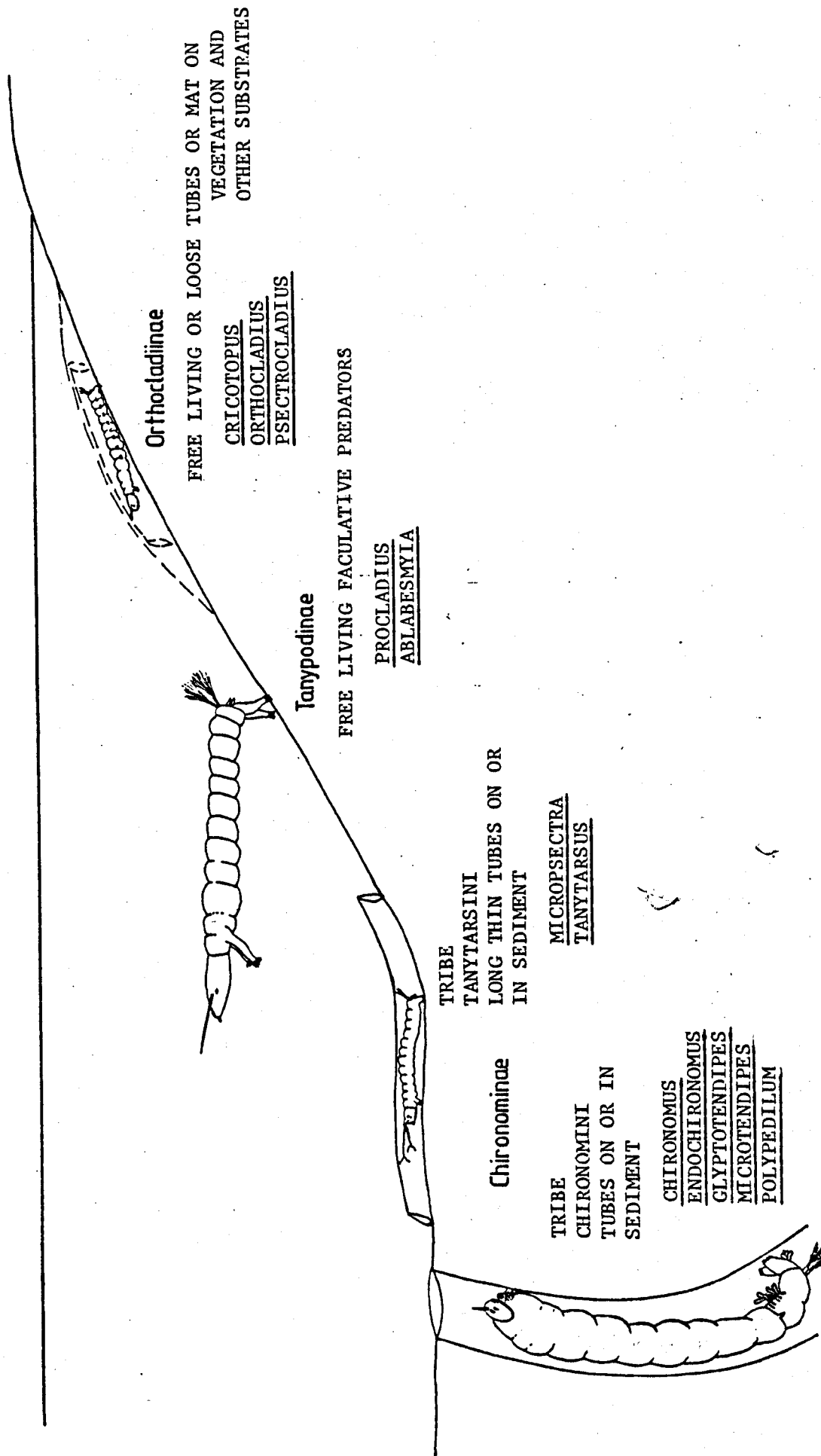


Fig. 32. Simplified pictorial representation of habits of the major subfamilies and genera of chironomid occurring at Rutland Water. (Positions do not indicate complete depth distributions)

habits of each of the major chironomid subfamilies and genera occurring at Rutland Water.

A total of 51 species was collected at the reservoir during the study period (Table 19). The list includes both the typical reservoir species, for example Procladius choreus, Psectrocladius sordidellus, Chironomus plumosus and Tanytarsus spp. as well as several which are atypical for this habitat, for example Eukiefferiella claripennis and Smittia spp. E. claripennis is a rheophilous species and the single larva found was almost certainly carried into the reservoir by one of the small inflowing streams. Several terrestrial species were also recorded as larvae in the reservoir; Smittia spp. and Pseudosmittia sp. The Smittia spp. were recorded as adults in sweep net samples and may not have occurred within the reservoir. Pseudosmittia sp. were recorded as pupal exuviae and these may have emerged after flooding of terrestrial vegetation.

b) Successional changes in chironomid fauna

Several sites which were considered to be potential sources for early invaders to the reservoir were investigated by Morton in 1975. Pond net samples were collected from the River Gwash in the vicinity of the reservoir, from March to June 1975. Ten genera of chironomid larvae were identified in these samples; Procladius, Ablabesmyia, Cricotopus, Orthocladius, Paracladius, Chironomus, Glyptotendipes, Endochironomus, Polypedilum and Tanytarsus. Burley fish ponds, located at the western end of the north-arm of the reservoir and inundated in Spring 1977, were also sampled in April 1975. Procladius, Chironomus and Cryptochironomus larvae were identified.

The earliest samples collected from the reservoir were in January, May and June 1975, by Morton, using a pond net. Eight of the ten genera previously recorded in the River Gwash were found; Orthocladius and Paracladius were the exceptions. The most commonly occurring genera in these reservoir samples were

Table 19: Chironomid species list for Rutland Water, 1976 to 1979, compiled from larval, pupal exuvial and adult male collections. A question mark before the second term of the binomial name indicates uncertain species identification.

	Larvae	Pupae	Adults
TANYPODINAE			
Macropelopiini			
1. Procladius choreus gr.	X	X	X
2. Procladius sp 1		X	
3. Psilotanypus ruffovittatus (Wulp)		X	X
Pentaneurini			
4. Ablabesmyia monilis (Linnaeus)		X	X
5. Ablabesmyia phatta (Egger)		X	X
ORTHOCLADIINAE			
Orthocladiini			
6. Cricotopus bicinctus (Meigen)	X		
7. Cricotopus trifascia Edwards	X		
8. Cricotopus intersectus (Staeger)	X		
9. Cricotopus sylvestris gr.	X	X	X
10. Cricotopus tricinctus (Meigen)	X		
11. Eukiefferiella claripennis (Lundbeck)	X		
12. Orthocladius consobrius (Holmgren)	X	X	X
13. Orthocladius glabripennis Goetghebuer			X
14. Orthocladius oblidens (Walker)	X		X
15. Orthocladius thienemanni Kieffer		X	
16. Paracladius conversus (Walker)	X		
17. Psectrocladius barbimanus (Edwards)	X	X	X
18. Psectrocladius sordidellus (Zetterstedt)	X		X
Metriocnemini			
19. Bryophaenocladius nitidicollis (Goetghebuer)			X
20. Chaetocladius sp 1		X	
21. Corynoneura carriana Edwards			X
22. Corynoneura sp 1		X	
23. Metriocnemus atratulus (Zetterstedt)			X
24. Metriocnemus hygropetricus (Kieffer)		X	X
25. Pseudosmittia sp 1		X	
26. Smittia ?edwardsi Goetghebuer			X
27. Smittia pratorum (Goetghebuer)			X

Table 19: (Continued)

	Larvae	Pupae	Adults
CHIRONOMINAE			
Chironomini			
28. <i>Camptochironomus tentans</i> (Fabricus)			X
29. <i>Chironomus ?longistylis</i> Meigen			X
30. <i>Chironomus plumosus</i> (L.)			X
31. <i>Chironomus riparius</i> Meigen			X
32. <i>Cryptochironomus supplicans</i> (Meigen)		X	
33. <i>Einfeldia</i> sp 1	X		
34. <i>Endochironomus albipennis</i> (Meigen)		X	X
35. <i>Glyptotendipes ?gripekoveni</i> (Kieffer)		X	
36. <i>Glyptotendipes pallens</i> (Meigen)		X	X
37. <i>Glyptotendipes paripes</i> (Edwards)		X	X
38. <i>Limnochironomus nervosus</i> (Staeger)			X
39. <i>Microtendipes chloris</i> (Meigen)			X
40. <i>Parachironomus arcuatus</i> (Goetghebuer)			X
41. <i>Parachironomus parilis</i> (Walker)			X
42. <i>Parachironomus vitiosus</i> (Goetghebuer)			X
43. <i>Polypedilum nubeculosum</i> (Meigen)		X	X
Tanytarsini			
44. <i>Micropsectra lindrothi</i> Goetghebuer		X	X
45. <i>Tanytarsus bathophilus</i> Kieffer			X
46. <i>Tanytarsus gracilentus</i> Holmgren			X
47. <i>Tanytarsus gregarius</i> Kieffer			X
48. <i>Tanytarsus lestagei</i> gr.		X	X
49. <i>Tanytarsus longitarsus</i> (Kieffer)		X	
50. <i>Tanytarsus pallidicornis</i> (Walker)		X	X
51. <i>Tanytarsus holochlorus</i> Edwards			X

Chironomus and Procladius. The first records for 1976 were obtained in March by examining the contents of one rainbow trout stomach and one brown trout stomach, collected by Harper. Orthocladius, Microtendipes and Psectrocladius larvae were recorded, the latter being the most abundant. In April and May 1976, dredge samples were collected by Bullock. Procladius and Polypedilum larvae were the most abundant genera recorded (Table 20). Larger numbers of larvae of most genera were found in the north- and south-arms of the reservoir than in the central basin. The Orthoclaadiinae are shallow water species (see Fig. 32) and are underestimated in these dredge samples as the haul was not started at the reservoir margin.

The changes in the relative proportions of the major genera, from June 1976 to April 1979, are shown in Figure 33. The data are based on all transects that were sampled each month using the two grab samplers. The sampling schedule has been given in Table 5.

In June 1976 Psectrocladius and Cricotopus larvae were abundant and together they formed 54% of the total recorded chironomid fauna. By October of that year they had disappeared from samples and Chironomus (48%) and Polypedilum (25%) predominated.

From May to September 1977 only the second north-arm and second south-arm transects were sampled. A number of changes in the proportions of different genera probably reflect this change in sampling. These two transects are located at the shallow western end of the reservoir (Fig. 16) and had only recently been inundated. Thus, the observed increase in proportion of Orthoclaadiinae larvae would be expected due both to the shallow water and the nature of the substrate, mainly composed of terrestrial vegetation covered with epilithic algae. The proportion of Chironomini larvae would be expected to decrease due to the thin sediment layers preventing tube formation. The proportion of Orthocladius larvae were observed to increase

Table 20: Numbers of larvae recorded in 50m dredge hauls

Genera	April 1976				May 1976		
	North-Arm	Dam	North-Arm to Tower	North Bay of Central Basin	North-Arm	South Bay of Central Basin	South-Arm
Procladius	10	6	64	6	52	9	54
Ablabesmyia	1			1	27		1
Cricotopus			1				
Psectrocladius	12		2	4	5		4
Chironomus		2	16				2
Cryptochironomus		1	3	6	16	4	4
Endochironomus	1		7	2	5	3	22
Glyptotendipes			2		13	2	6
Microtendipes	2						
Polypedilum	13	23	16	13	108	3	27
Tanytarsini	7	3			1		1

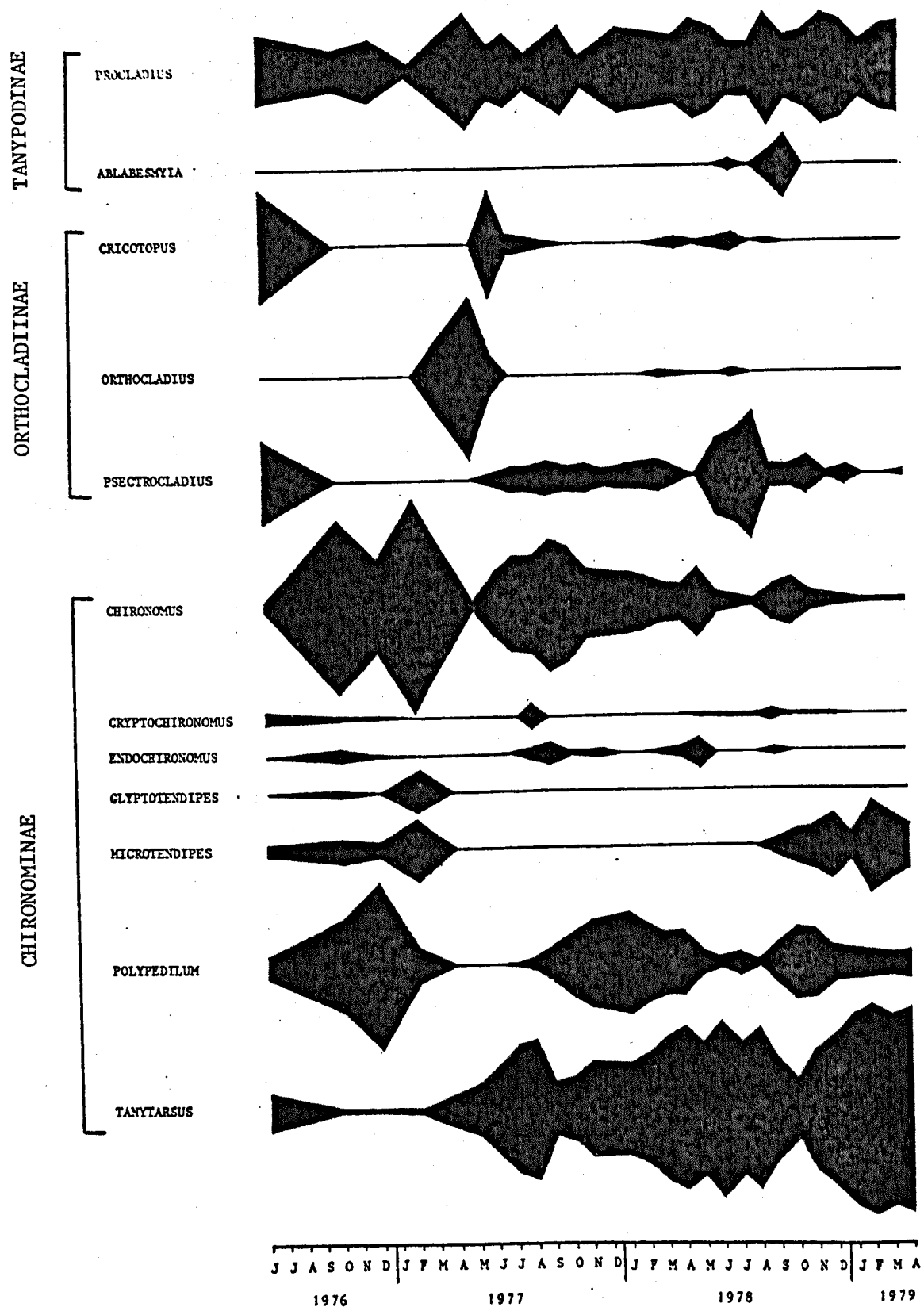


Fig. 33. Changes in the proportions of the major genera based on larvae.

dramatically during this period whilst the proportion of Chironomus larvae decreased (Fig. 33). The unrepresentative nature of these two transects is supported by data from dredge samples taken in the two arms and in the central basin in June, July and August 1977. Although the results cannot be compared quantitatively with those from the grab samples they do indicate the relative abundance of different species. Chironomus, Endochironomus and Polypedilum larvae were all found in relatively large numbers in these samples (Table 21). Endochironomus larvae were particularly abundant in July and August in these dredge samples but were not recorded at all in the grab samples taken along the second north-arm and second south-arm transects.

All six transects were sampled monthly from September 1977 to April 1979, except for three months in which the sampling programme was affected by adverse weather conditions, December 1978, January and February 1979 (Table 5). The observed proportion of Procladius larvae remained approximately the same throughout the whole of 1977 and 1978 whilst the other Tanypodinae genus, Ablabesmyia, was found only at the end of 1978 (Fig. 33). Of the three Orthocladiinae genera Psectrocladius predominated in summer samples during 1978. Chironomus larvae declined gradually in the samples from September 1977 to April 1979 whilst Microtendipes larvae showed an increase in proportion at the end of 1978. Tanytarsus larvae increased in proportion throughout the period and by April 1979 were the dominant group.

To summarise changes at the specific level recorded from larval samples, Procladius choreus gr. and Ablabesmyia spp. have been recorded since the early stages of inundation although there have been seasonal fluctuations in population densities. Orthocladiinae larvae showed considerable seasonal fluctuations and changes in species composition and population density. Cricotopus bicinctus and Cricotopus tricinctus were recorded in June 1976 but were not found in the following years.

Table 21: Numbers of larvae from 50m dredge hauls

	14.6.77		21.6.77		27.7.77		15.8.78	
	North -Arm	South -Arm	North -Arm	South -Arm	North -Arm	South -Arm	North -Arm	South -Arm
Procladius	5	2	39		13		2	1
Ablabesmyia	18	2	1	7				
Cricotopus					12			
Orthocladius					1			
Psectrocladius					23			
Chironomus			1		33	1	2	1
Cryptochironomus	1	1	2		3			
Endochironomus	1	6		1	107	12	61	95
Glyptotendipes	2			1	1			1
Microtendipes								
Polypedilum			5		3			4
Tanytarsini					21			3
								1
								25
								1

Orthocladius thienemanni was recorded in January and February 1978 but was not recorded previously or subsequently. Large numbers of Paracladius conversus were found in 1976 but did not reappear in 1977, 1978 or 1979. Few species changes occurred in the Chironomini. Camptochironomus tentans, Limnochironomus nervosus and Parachironomus parilis were all recorded in 1978 but had not been recorded previously. Einfeldia sp. was recorded in the early development of the reservoir but has not been found in samples since Spring 1978. The Tanytarsini larvae are difficult to separate as larvae and little information is available other than from pupal exuviae and adult collections.

c) Seasonal population estimates

Population estimates for the eight most consistently abundant taxa, together constituting over 90% of the observed chironomid fauna, were calculated using data from grab samples taken along all six transects (see Fig. 16 for locations). The samples were grouped into four depth zones, 0-5m, 6-10m, 11-15m and deeper than 16m. The mean population densities were calculated for each depth zone. By grouping the data into depth zones the sample variance caused by depth distributions is reduced. The disadvantage of the method results from different numbers of sampling units being taken in each of the depth zones. The sampling schedule and number of sampling units (grab samples) collected within each depth zone have been given in Table 5. Fluctuations in water level may also result in populations being recorded in deeper or shallower water than usual. Figure 9 shows the major fluctuations in water level and likely effects of these fluctuations are noted in the text.

Procladius

Procladius choreus (Meigen) has been treated as one species although the taxonomy is under review by Aagard (pers. comm.) who considers it to be a species group of 7 or 8 species. Analysis of pupal exuviae at Rutland Water indicates the presence of two species of Procladius, the predominant one being P. choreus; the

second has not been identified. Psilotanypus rufovittatus was also recorded in exuvial and adult samples (Tables 22 and 23) and the larvae may have been identified as Procladius. However, this is unlikely to make a significant difference to the results as P. ruf ovittatus represented less than 3% of the combined Procladius and Psilotanypus exuviae in collections made from October 1977 to October 1978 (Table 22).

Considering the entire depth profile, Procladius was particularly abundant during the winter of 1977-78 ($\bar{x} = 193\text{m}^{-2}$) compared with the winters of 1976-77 ($\bar{x} = 65\text{m}^{-2}$) and 1978-79 ($\bar{x} = 162\text{m}^{-2}$) (Fig. 34). The high population density for the 1978-79 winter period is probably misleading on account of the small number of sampling units in the January 11-15m depth zone. Similar fluctuations in density were recorded from the 0-5m and 6-10m depth zones, although higher numbers were recorded in the 6-10m zone (mean July 1976 to April 1979 279m^{-2}) than in the 0-5m zone (mean July 1976 to April 1979 166m^{-2}). The greatest monthly fluctuations in numbers was recorded in the 11-15m depth zone. This may be due to the small numbers of samples upon which some of the data are based (Table 5). Over the whole sampling period the mean density at depths greater than 16m was relatively low at 71m^{-2} .

The marked decline in numbers in June, July and August 1978 is probably due to emergence and this is supported by evidence from exuviae which were recorded from May to October 1978 (Table 22); with the largest numbers at the end of August 1978. This is a similar period to that recorded by Mundie (1957) and Potter and Learner (1974) who both considered P. choreus to be bivoltine. Spatial variation in the timing of emergence was also noted by these authors, emergence from deeper water occurring later than from shallow water. In Rutland Water no clear evidence is available to confirm P. choreus as bivoltine. However, a decline in larval population density was recorded in May 1978 at all depths and a major decline in August 1978, these could possibly correspond to two periods of emergence. However, this

	Sampling Dates																Total Numbers	% Numbers
	24.10.77	29.11.77	16. 1.78	28. 2.78	7. 3.78	29. 3.78	21. 4.78	29. 4.78	9. 5.78	17. 5.78	31. 5.78	10. 6.78	27. 6.78	16. 8.78	29. 8.78	23.10.78		
<i>Procladius choreus</i>	2								+		5	12	5	1	(15)	3	95	3
<i>Psilotanypus ruf ovittatus</i>											+				(+)		3	+
<i>Ablabesmyia monilis</i>											6	3	(19)	12	16		163	5
<i>Ablabesmyia phatta</i>													+	2	(5)		21	+
<i>Cricotopus sylvestris</i>	1						+	2	2		1	29	(13)		4	2	115	3
<i>Cricotopus sp. 1</i>	2								4		2		(7)				51	2
<i>Orthocladius consobrinus</i>	8					10	3	1	+		+	(23)	5			2	105	3
<i>Orthocladius sp. 1</i>				2	(1)												5	+
<i>Orthocladius sp. 2</i>	+												(+)				5	+
<i>Orthocladius sp. 3</i>	+	3	80	95	(89)	80	14	2	20		7		4				752	22
<i>Psectrocladius barbimanus</i>	4						5	18	2	27	+	13	(14)	2	4	24	212	6
<i>Psectrocladius sordidellus</i>	(4)						+					+					10	+
<i>Corynoneura spp.</i>											1		+		2	(24)	52	2
<i>Chaetocladius sp.</i>			7		1	(1)										1	8	+
<i>Metriocnemus spp.</i>		3			(4)	2	+										15	+
<i>Pseudosmittia sp.</i>						(+)											1	+
<i>Chironomus plumosus gr.</i>	2						2	7	5	48	13	+	+	(50)	8	1	247	7
<i>Chironomus riparius gr.</i>	7	61					(5)	6	+			4	1	6	3	1	109	3
<i>Cryptochironomus sp.</i>													4	(2)			6	+
<i>Endochironomus sp.</i>										18	(16)	16		1	7		87	3
<i>Glyptotendipes sp.</i>											+	(5)		+			7	+
<i>Microtendipes chloris</i>							(15)	9	9	7	+		+	9	15		225	6
<i>Parachironomus sp.</i>											2	+	(2)				11	+
<i>Polypedilum nubeculosum</i>									4		6		2	2	(5)		54	2
<i>Micropsectra sp.</i>	(16)	32	7	4	6	5	1	+	+			+					83	2
<i>Tanytarsus lestagei</i>	14	3	7			+	(50)	40	35				3	11	14	43	696	20
<i>Tanytarsus pallidicornis</i>						+	(1)	+									11	+
<i>Tanytarsus sp. 1</i>	3						2	11	(16)			2	18	+	2		189	5
<i>Tanytarsus sp. 2</i>	(19)												3				41	1
<i>Tanytarsus sp. 3</i>	(4)																7	+
<i>Tanytarsus sp. 4</i>									1		(41)						85	2
Total Numbers	166	38	15	110	283	210	609	189	455	60	197	107	383	204	327	119	3472	100
Number of Sampling Sites	2	1	3	2	7	7	8	4	8	2	7	2	6	6	6	2		

Table 22: Chironomid pupal exuviae collected at sites around Rutland Water in 1977 and 1978 expressed as a % occurrence for each date. (+) % number less than 1; (o) indicates date on which the greatest numbers of each species were collected.

	Sampling dates																	
	23. 6.77	24. 8.77	10. 9.77	22. 9.77	23. 9.77	29. 9.77	21. 4.78	9. 5.78	17. 5.78	31. 5.78	10. 6.78	13. 6.78	27. 6.78	16. 8.78	19. 8.78	29. 8.78	23.10.78	
<i>Procladius choreus</i>			1	13	4	17					(8)			1				
<i>Psilotanypus ruf. ovittatus</i>											(2)							
<i>Ablabesmyia monilis</i>			1								1				(13)			
<i>Ablabesmyia phatta</i>											(3)							
<i>Cricotopus sylvestris</i>									(9)	+	7	2	1	1		3		
<i>Cricotopus intersectus</i>													+	(+)				
<i>Orthocladius ?oblidens</i>	16							+	(21)	+			+					
<i>Orthocladius glabripennis</i>								(1)										
<i>Psectrocladius barbimanus</i>			7				8	+	3	1			(5)	+		6	1	
<i>Psectrocladius sordidellus</i>																(3)		
<i>Metriocnemus hygropteticus</i>	(2)																2	
<i>Bryophaenocladius nitidicollis</i>													(+)					
<i>Smittia pratorum</i>						15								+			(4)	
<i>Camptochironomus tentans</i>					4									(1)	2	3		
<i>Chironomus plumosus</i>		7	15	25	8			1	4	+	(12)					3		
<i>Chironomus riparius</i>	(23)		14	38				+									1	
<i>Chironomus longistylus</i>							4				(+)			+	2			
<i>Endochironomus albipennis</i>			(24)	13						+	2							
<i>Limnochironomus nervosus</i>										(+)								
<i>Glyptotendipes paripes</i>										+	(1)							
<i>Parachironomus arcuatus</i>			11							+	(1)							
<i>Parachironomus vitiosus</i>											(1)							
<i>Microtendipes chloris</i>			1			(12)												
<i>Polypedilum nubeculosum</i>			7		8			2	(22)	+	1		1	+	3	3		
<i>Micropsectra lindrothi</i>	3										+	(30)						
<i>Tanytarsus gracilentus</i>	48	93		13	60		12	(85)	8	1	58	69	91	} 91		26	87	
<i>Tanytarsus bathophilus</i>			1		8	73	50	8	(30)	+			1			80		2
<i>Tanytarsus lestagei</i>			16		8			2	(93)			1			+	2	3	
<i>Tanytarsus pallidicornis</i>	(7)		2						+									
<i>Tanytarsus holochloris</i>			+			(20)												

Table 23: Percentage occurrence of adult male chironomids collected around Rutland Water from June 1976 to October 1978. (+) % number less than 1; (o) indicates date on which the greatest numbers of each species were collected.

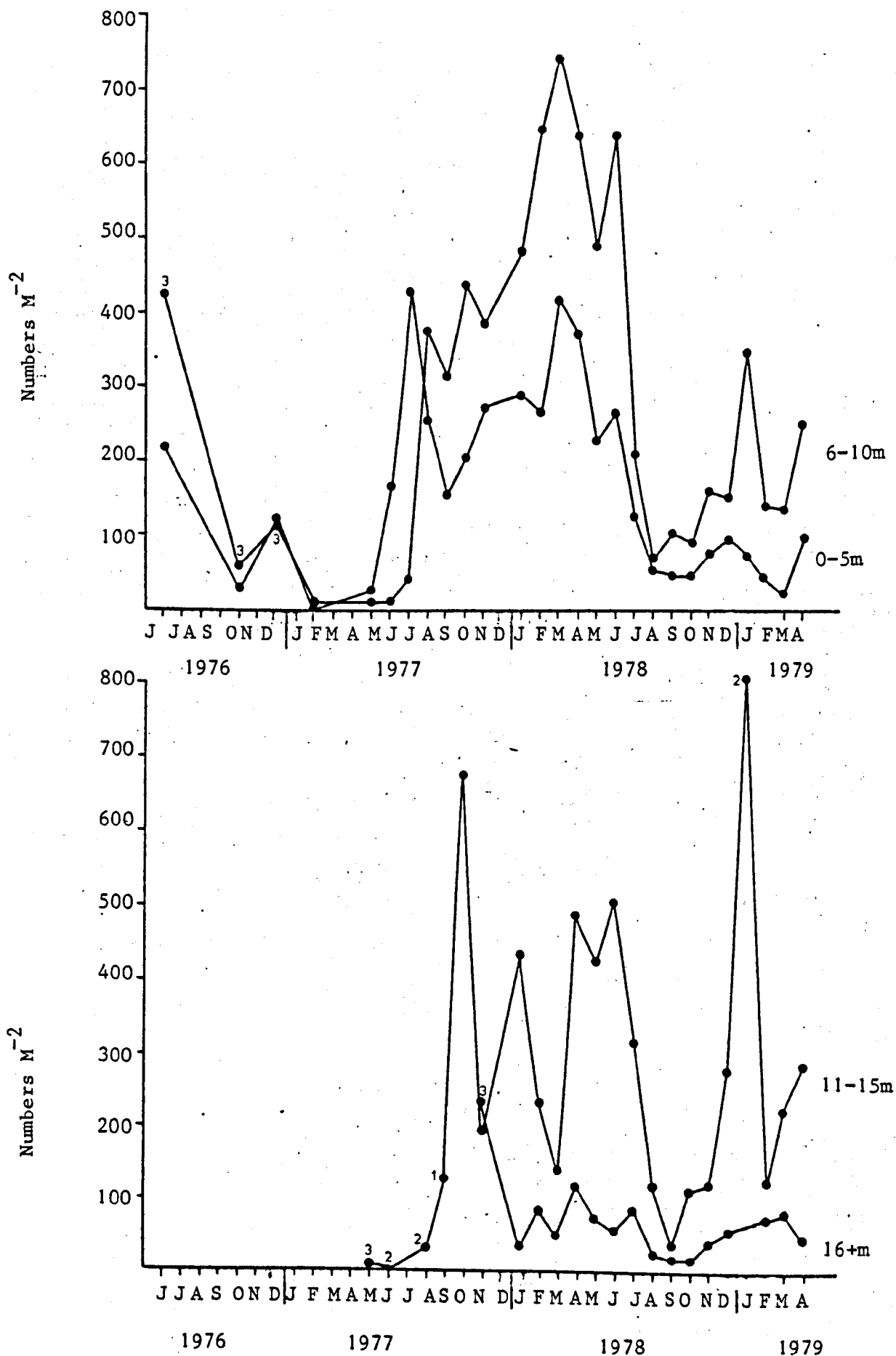


Fig. 34. Monthly population densities of *Procladius* for four depth zones. Actual numbers of grab samples given for points where < 5 grab samples used to calculate mean. For complete sampling schedule see Table 5.

is a subjective assessment as no emergence trapping or detailed investigations of life histories are available to confirm emergence.

Cricotopus

Five species of Cricotopus have been identified at Rutland Water; C. sylvestris, C. bicinctus, C. intersectus, C. tricinctus and C. trifascia. The larvae were not routinely identified to species but analysis of the pupal exuviae and adult data revealed the C. sylvestris group to be the most abundant (Tables 22 and 23).

Large populations occurred each summer in shallow water (Fig. 35). Low population densities ($<2\text{m}^{-2}$) were recorded in the 6-10m depth zone and only isolated individuals were found in deeper water. The maximum population densities were recorded in July 1976 and overwintering populations were very small.

Pupal exuviae were recorded from April to October 1978 with the largest numbers occurring in June (Table 22). Mundie (1957) found 3 generations per year for C. sylvestris at eutrophic Kempton Park reservoir, England, with emergences occurring in May, July and September. Exuviae collected during 1978 indicate that several generations may have occurred at Rutland Water. A more restricted emergence period and earlier main emergence was recorded for both C. sylvestris and C. intersectus in a gravel pit studied by Titmus (1979).

Psectrocladius

Two species of Psectrocladius were identified at Rutland Water, P. sordidellus and P. barbimanus. In 1977 P. sordidellus, identified from larval specimens, was the predominant species. Pupal exuvial analysis, however, revealed P. barbimanus to be the predominant species in 1978 (Table 22). The identification of both the larvae and adults of this genus to the species level is difficult and hence the two species have been treated together.

Fig. 35. Monthly population densities for Cricotopus for four depth zones. Actual number of grab samples given for points where 5 grab samples were used to calculate mean. For complete sampling schedule see Table 5.

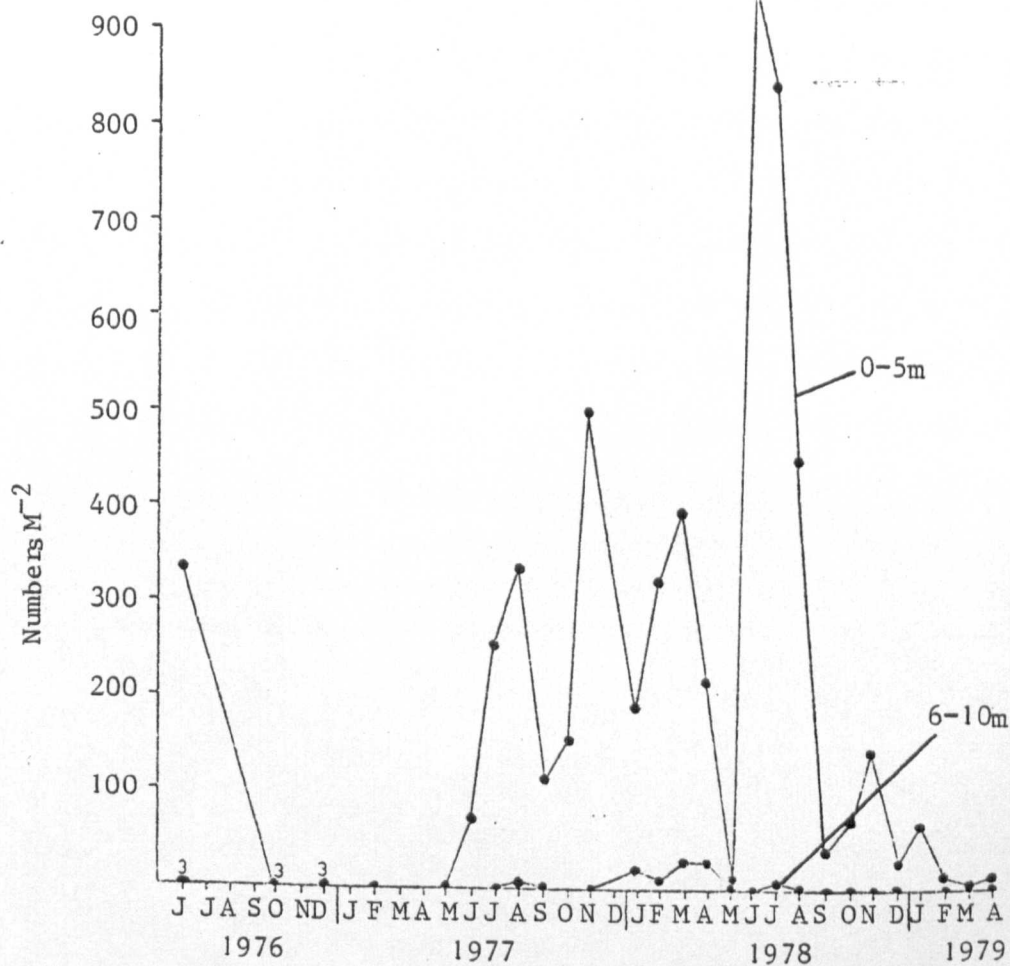
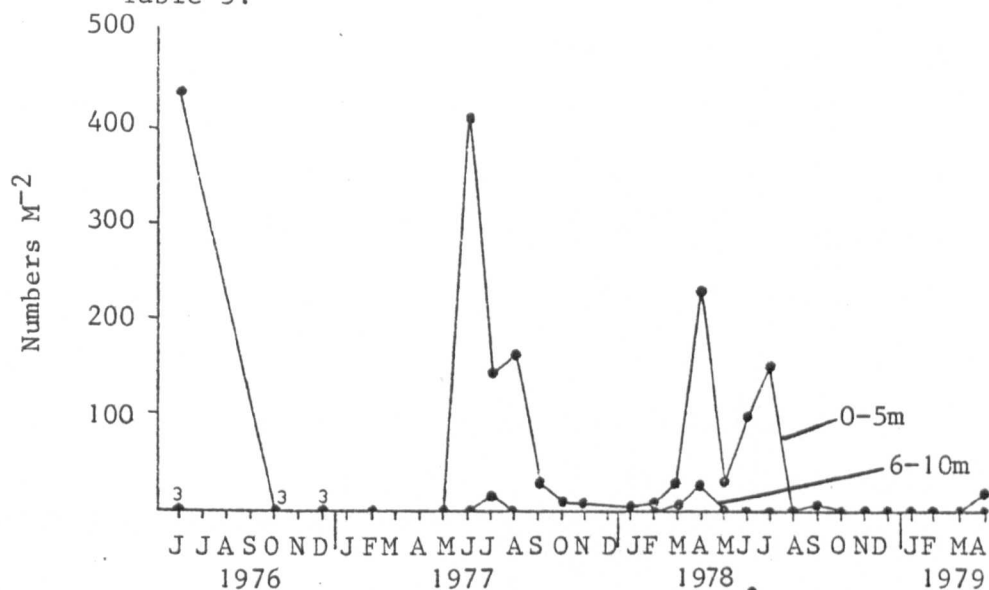


Fig.36. Monthly population densities of Psectrocladius for four depth zones. Actual number of samples given for points where <5 grab samples used to calculate mean. For complete sampling schedule see Table 5.

The population density of Psectrocladius in the 0-5m depth zone was highly variable (Fig. 36). Population densities were low at greater depths. Overwintering populations were low in 1976-77 and 1978-79 but high in 1977-78.

Pupal exuviae of P. barbimanus were recorded from April to October 1978 and the largest numbers occurred in June (Table 22). Larval data for 1978 suggests an emergence in May, possibly of the overwintering generation, and a second emergence in August and September, possibly of the summer generation (Fig. 36). Similar emergence periods were recorded for P. barbimanus by Mundie (1957).

Chironomus

In 1977, analysis of adult males revealed the ratio of the C. plumosus group to the C. riparius group as approximately 100:1. In 1978, however, this ratio had changed to approximately 1:1, mainly as a result of the decline in numbers of the C. plumosus group. Identification of adults revealed the species to be C. plumosus and C. riparius sensu stricto (Table 23). Isolated individuals of C. ?longistylis were also found.

The population density of Chironomus rapidly increased from May to July 1977, and a maximum population density of 864m^{-2} was recorded in the 0-5m depth zone (Fig. 37). Since then the population density has gradually declined with a particularly low overwintering population in 1978-79. A similar decline was recorded in all four depth zones.

A long emergence period was indicated for both species of Chironomus from the pupal exuvial and adult analysis (Tables 22 and 23). C. plumosus has been recorded as bivoltine by both Mundie (1957) at Kempton Park reservoir and Potter and Learner (1974) at Eglwys Nuny dd reservoir. Two generations a year in shallow water and one in deep water have been recorded by Borutzky (1939) and Johnson and Munger (1930). Mundie (op. cit.)

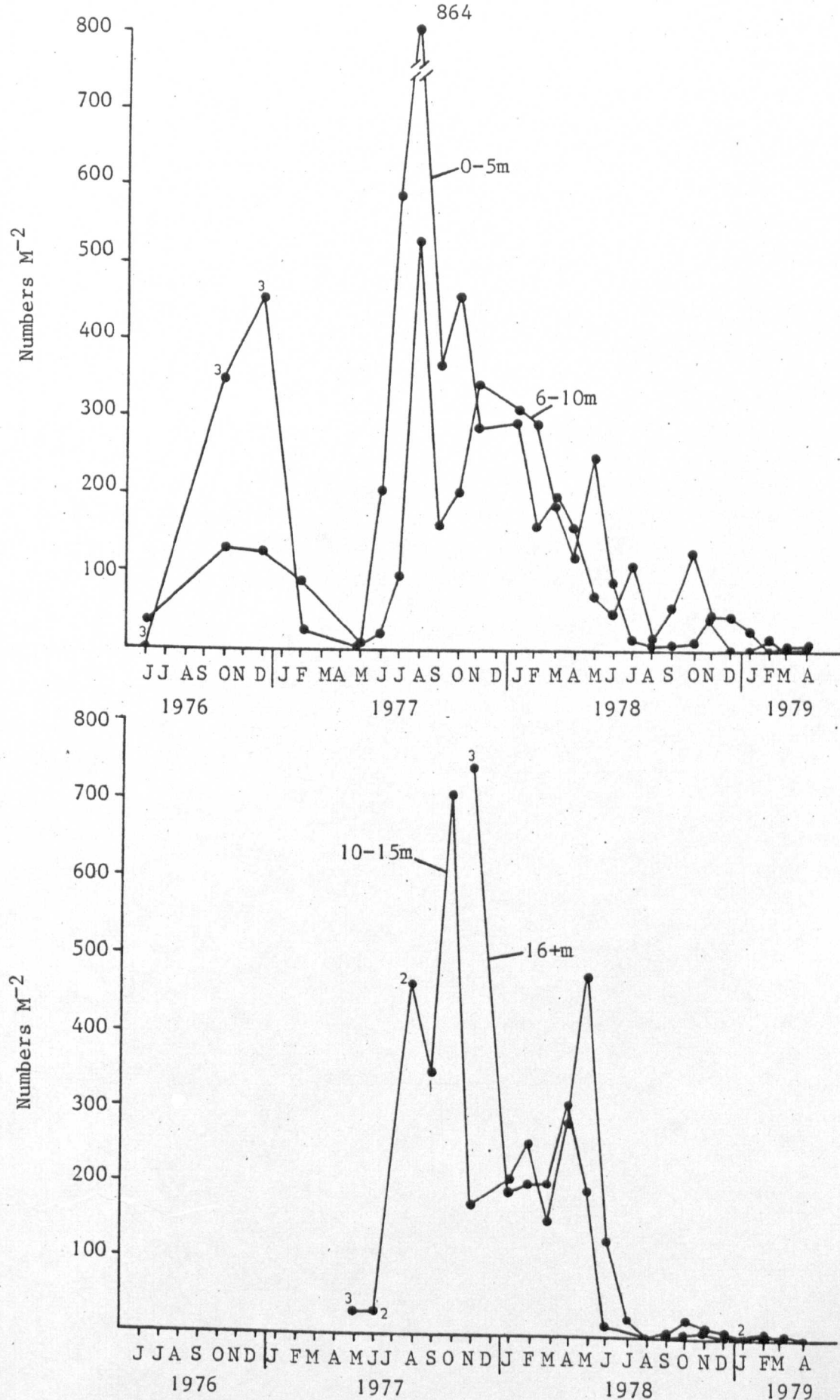


Fig. 37. Monthly population densities of Chironomus for four depth zones. Actual number of grab samples given for points where <5 grab samples were used to calculate the mean. For complete sampling schedule see Table 5.

recorded adult males of C. riparius swarming in June and again in October, thus, suggesting two periods of emergence for this species. The detection of emergence periods of Chironomus at Rutland Water is masked by the steady decline in populations throughout the study and is complicated by the presence of more than one species.

Endochironomus

Only one species of Endochironomus has been recorded at Rutland Water as larva, pupa or adult, E. albipennis. Throughout the sampling period the highest population densities were recorded in the 0-5m depth zone (Fig. 38). Few larvae were recorded in water greater than 10m except for an unexplained peak in April and May 1978. The decline in larval numbers in June 1978 (Fig. 38) and the large numbers of exuviae found in May 1978 (Table 22) indicate that this was the main emergence period. Pupal exuviae were found until the end of August 1978 although no adult males were collected after June (Table 23). Populations remained low after the emergence period in 1978. Mundie (1975) and Bracken and Murray (1973) found E. albipennis to be bivoltine with emergence occurring at the end of May and August. At Rutland Water populations did decline in May and again in August 1978 in the 0-5m depth zone and this may indicate the two emergence periods.

Microtendipes

M. chloris was the only species of Microtendipes recorded as larva, pupa or adult from Rutland Water. Low population densities were recorded in all depth zones on most sampling dates from the beginning of 1977 until September 1978 (Fig. 39). From September 1978 the population density increased in all depth zones to a maximum of 194m^{-2} in the 6-10m depth zone. M. chloris was the only species of the eight dominant chironomid taxa to show an increase in numbers after the summer emergence in 1978.

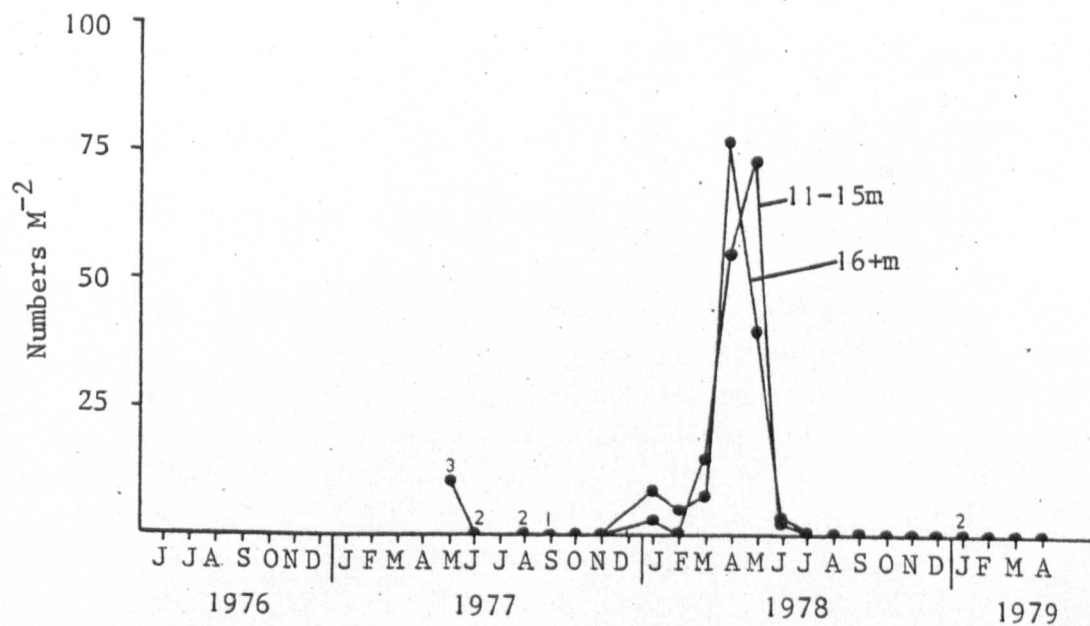
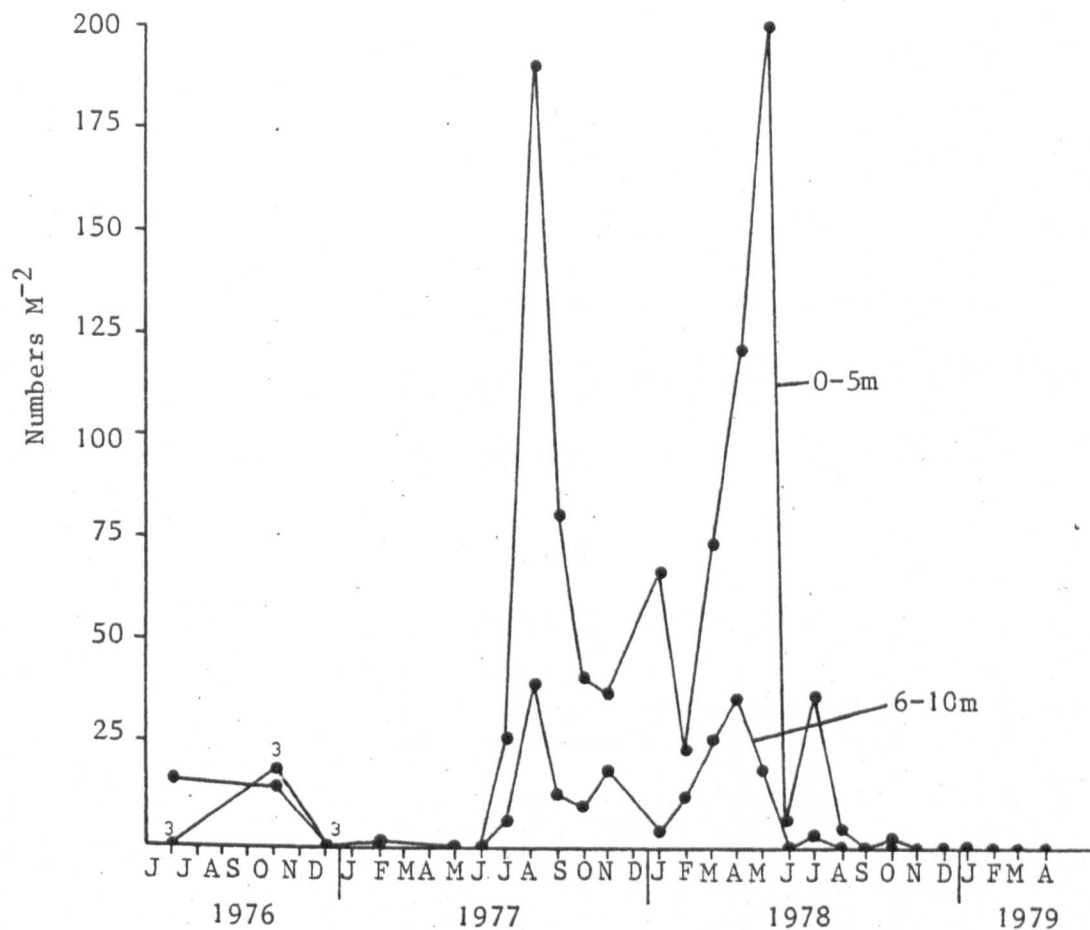


Fig. 38. Monthly population densities of Endochironomus for four depth zones. Actual number of grab samples given for points where ≤ 5 grab samples used to calculate the mean. For complete sampling schedule see Table 5.

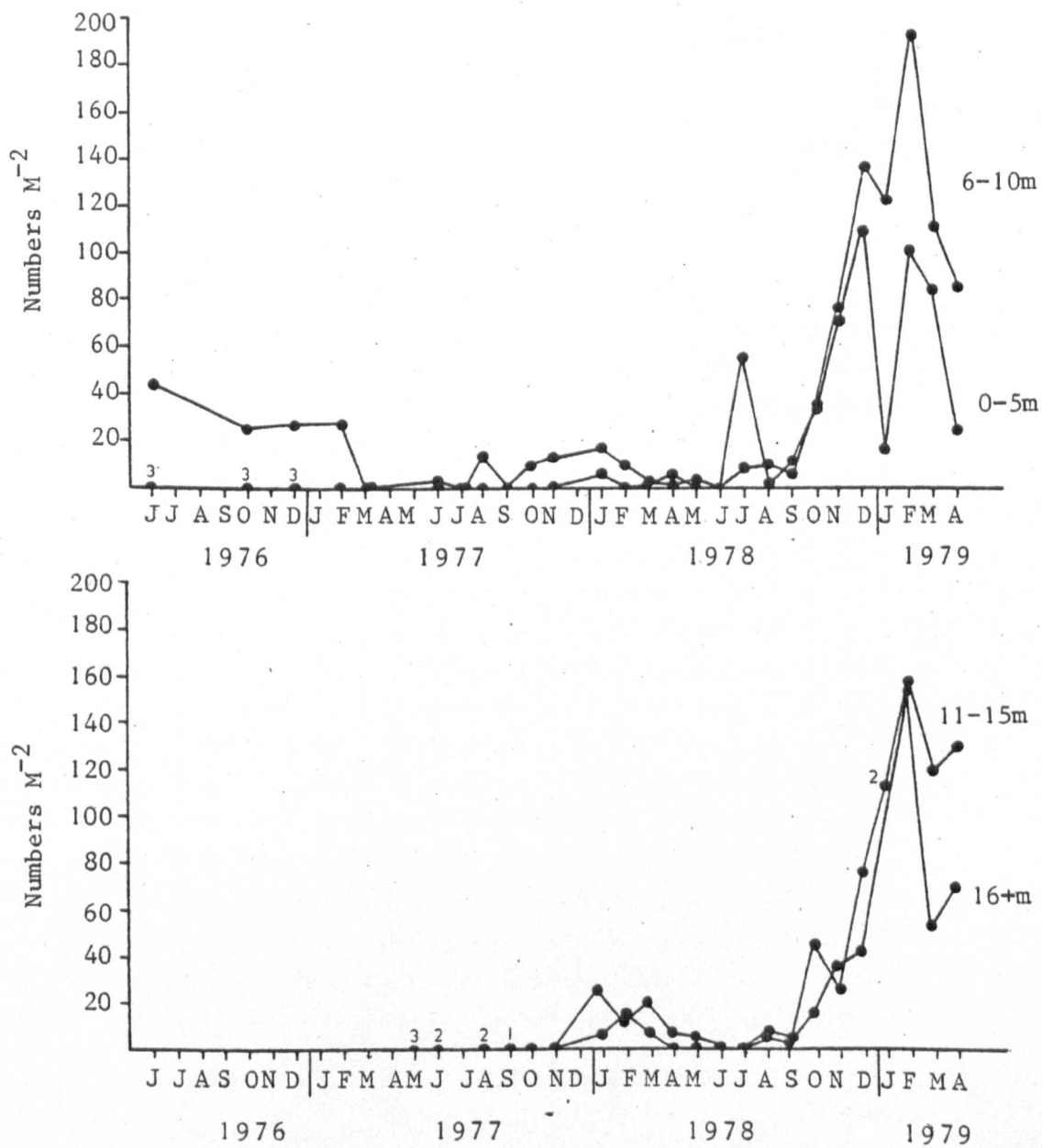


Fig. 39. Monthly population estimates of *Microtendipes* for four depth zones. The actual number of grab samples is given for points where < 5 grab samples were used to calculate the mean. For complete sampling schedule see Table 5.

Pupal exuviae were recorded from April 1978 to the end of August 1978 (Table 22). The high numbers of exuviae recorded in April were probably the result of the emergence of the overwintering larvae. Larval data suggest a second emergence period in August 1978. M. chloris was recorded as a Spring species and M. pedellus a Summer species by Mundie (1957). However, Potter and Learner (1974) suggest that these may be the same species. At Rutland Water the larvae, pupae and adults were all identified as one species. Thus, M. chloris is considered to be bivoltine and not univoltine as suggested by Mundie.

Polypedilum

P. nubeculosum was the only species recorded as larva, pupa or adult at Rutland Water. As in the case of Procladius larvae, the largest population densities were recorded during the winter period, 1977-78 (Fig. 40). Populations decreased in density in the deeper water. After the summer emergence in 1978 the populations did not increase to the same densities and overwintering populations were comparatively low in 1978-79.

The largest numbers of pupal exuviae were found at the end of August 1978 (Table 22). This coincides with the period of lowest larval densities. Adults and pupal exuviae were found from May to the end of August (Tables 22 and 23). Mundie (1957) recorded the main emergence periods of P. nubeculosum to be in May, July and September. At Rutland Water larval populations did show declines in February, May and August 1978 in the 0-10m depth zone (Fig. 40) and this may indicate three periods of emergence.

Tanytarsini

Two genera, Micropsectra and Tanytarsus, were not routinely separated as larvae and have been combined in these data. Only one species of Micropsectra has been recorded, M. lindrothi, whilst seven species of Tanytarsus were identified, T. gracilentus, T. gregarius, T. bathophilus, T. lestagei, T. pallidicornis,

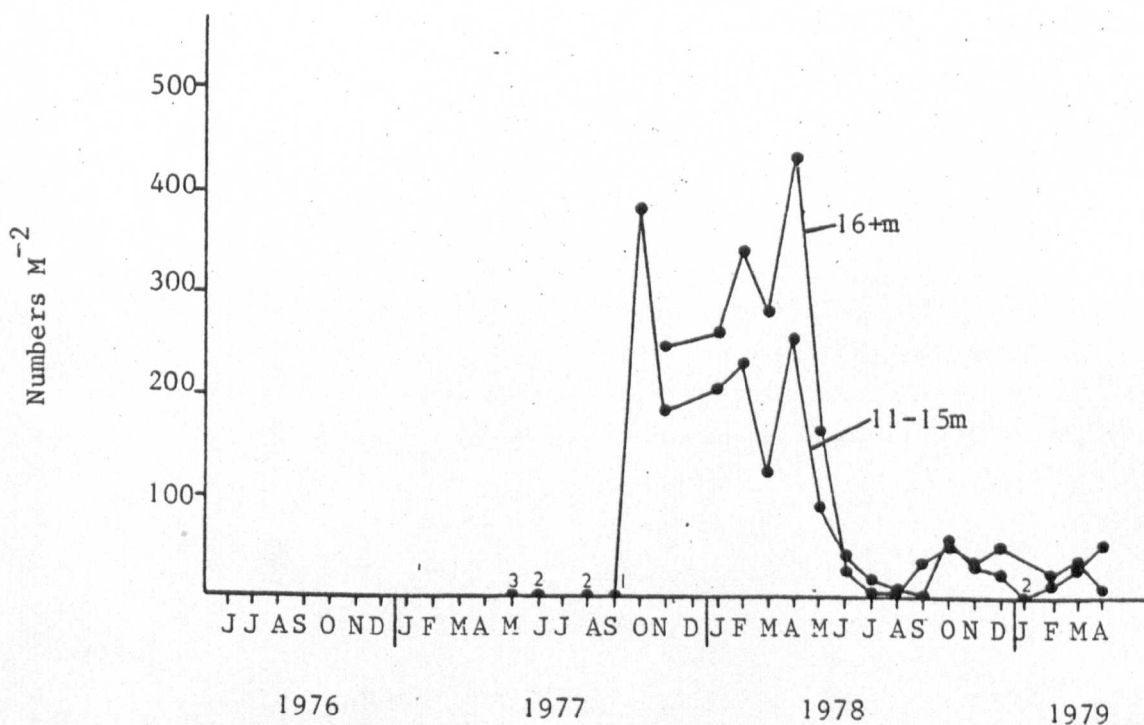
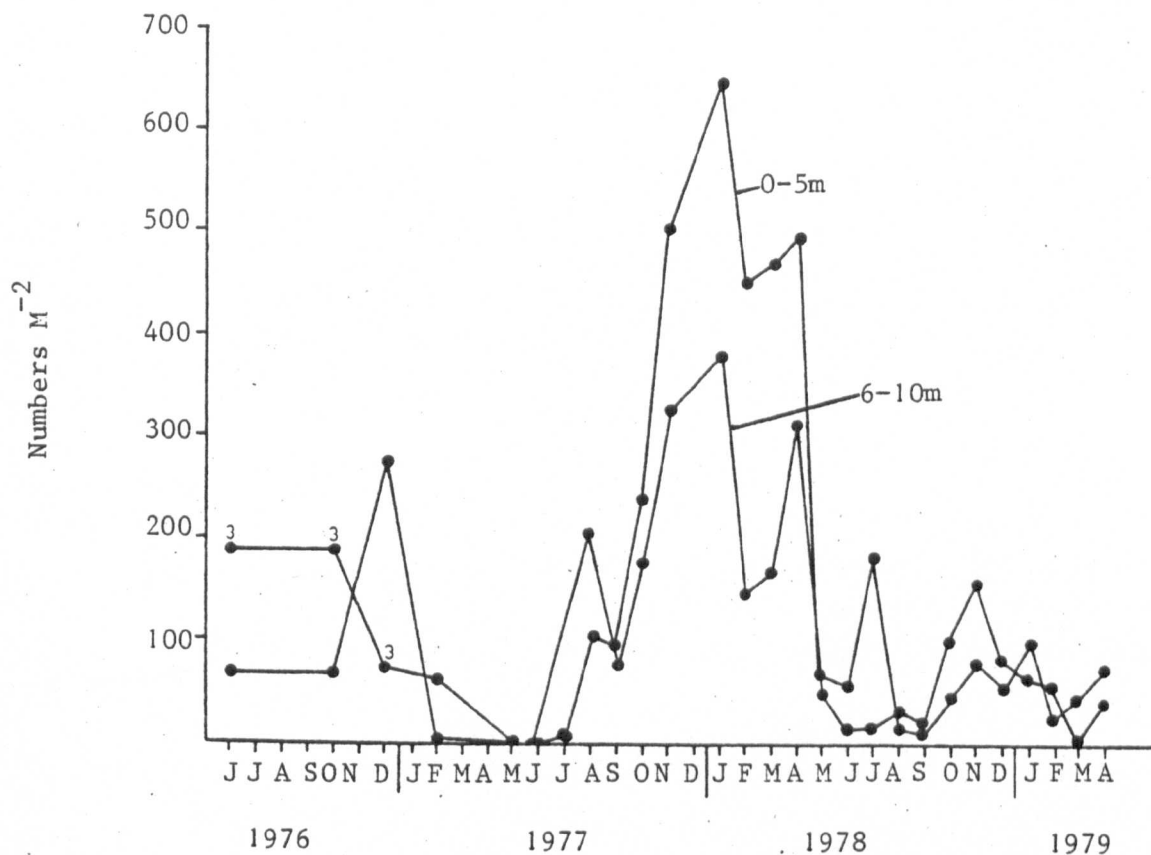


Fig. 40. Monthly population estimates of Polypedilum for four depth zones. Actual number of sampling units is given for points where <5 grab samples were used to calculate the mean. For complete sampling schedule see Table 5.

T. holochlorus, T. longitarsus. Pupal exuviae collected during 1978 (Table 22) indicate that Tanytarsus larvae were approximately 12 times more abundant than Micropsectra larvae and that T. lestagei was the most abundant species.

Tanytarsini larvae are the numerically dominant group in the reservoir samples. The average population density throughout the whole sampling period was 328m^{-2} compared with 201m^{-2} for Procladius larvae and 139m^{-2} for Chironomus larvae. The maximum population density was recorded in August 1977 in the 0-5m depth zone, $2,842\text{m}^{-2}$ (Fig. 41). Fluctuations in population density occurred in all depth zones and may be the result of different species emerging at different times.

Exuviae of M. lindrothi were recorded from October 1977 to May 1978 (Table 22) and the largest numbers occurred in October 1977. Only T. lestagei and T. pallidicornis were identified to the species level in pupal exuvial samples. The largest numbers of exuviae of both species were found in April 1978. The determination of the main emergence periods of the Tanytarsini larvae is impossible due to their collective treatment as larvae. Mundie (1957) found T. lestagei to be bivoltine with the main emergence occurring in August and September. T. holochlorus was also found to be bivoltine by Mundie (1957) and Potter and Learner (1974) with the main emergence period extending from May to October.

d) Annual changes in populations

Two main factors are thought to have influenced annual changes in the chironomid fauna. The first was the marked climatic differences that occurred between years (section c, Chapter 2). The second was the periodic nature of pumping and consequent changes in water level (Figs. 9 and 10).

The hot dry summer in 1976 resulted in high water temperatures and a relatively stable water level as little water was obtained either directly from the catchment or via pumped river water. This enabled extensive growths of benthic algae to develop and

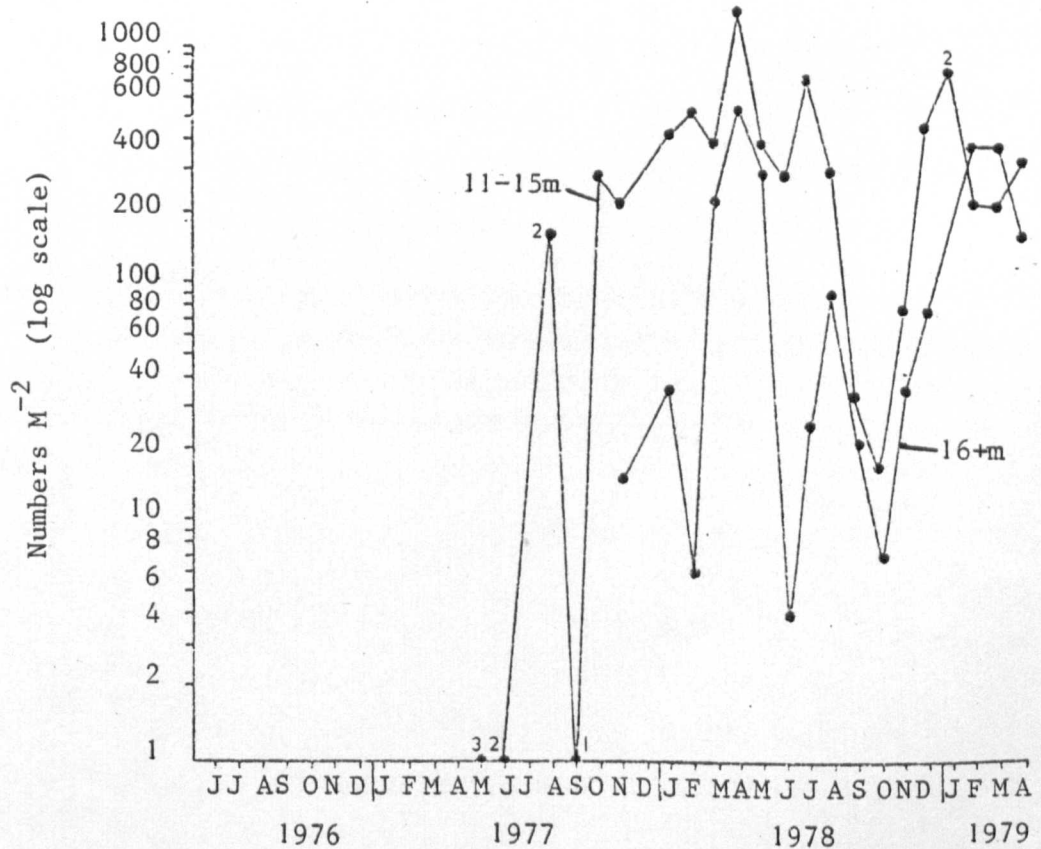
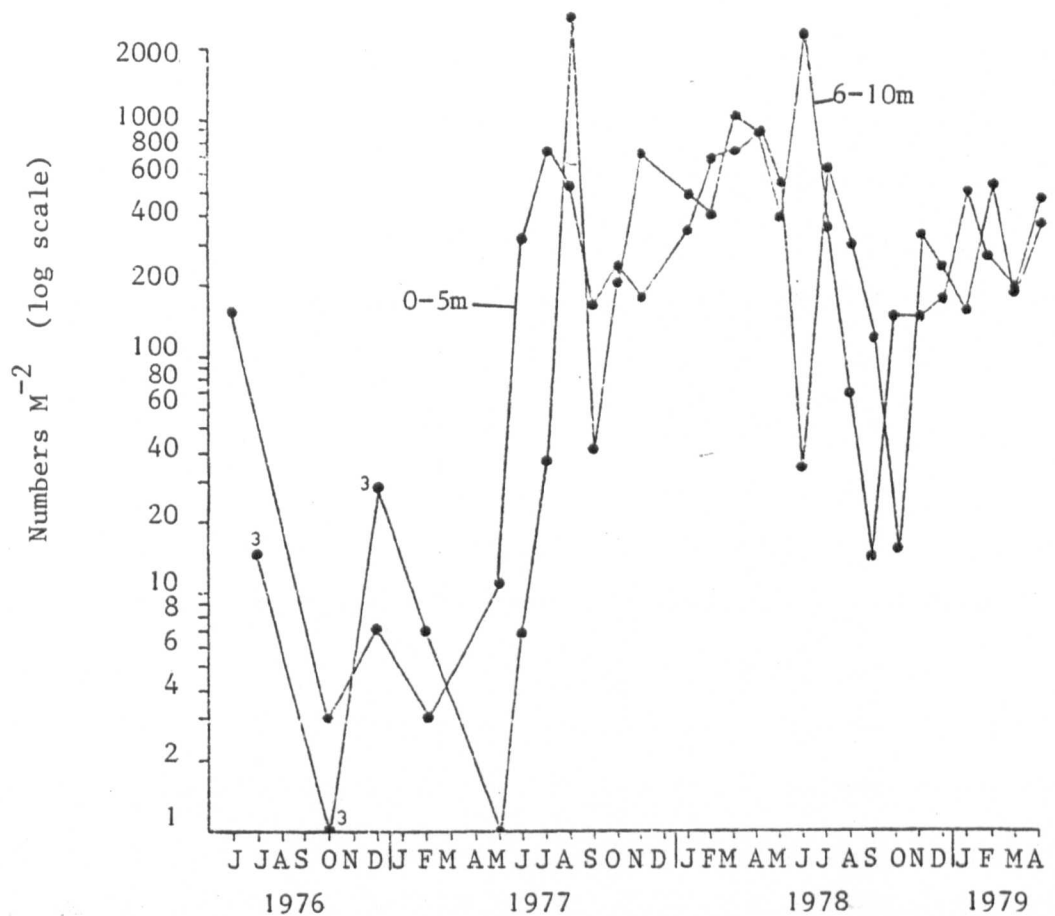


Fig. 41. Monthly population estimates of Tanytarsini for four depth zones. The actual number of sampling units is given for points where ≤ 5 grab samples were used to calculate the mean. For complete sampling schedule see Table 5.

these were colonised by Orthoclaadiinae larvae, particularly Cricotopus and Psectrocladius (Fig. 33). These larvae disappeared from the 1976-77 winter samples (Figs. 35 and 36) and this was thought to be the combined result of the seasonal decline in numbers together with the rapid rise in water level. This rise in water level would strand larvae in deep water and kill the algae, making conditions generally unfavourable for the group. Populations of Cricotopus and Psectrocladius did develop in the following years and the overwintering populations did not decline to such low densities. This may have been partly due to the relatively stable water level maintained throughout the remainder of the study period (Fig. 9).

In the early part of 1977 Orthocladus larvae were the predominant Orthoclaadiinae (Fig. 33). At this time only the second north-arm and second south-arm transects were sampled (Table 5) and they had only recently been flooded by the rapid influx of water during the winter. This suggests that certain species of the genus are rapid colonisers of new habitats. Comparatively few Orthocladus larvae were recorded throughout the remainder of the study.

In 1978 the numerically dominant taxa, excluding Microtendipes, all maintained comparatively low population densities after the summer emergence periods. Several hypotheses may be advanced to explain this result. Firstly, climatically 1978 was colder than previous years and low water temperatures may have increased the mortality of early instar larvae. Secondly, phytoplankton populations, as indicated by chlorophyll-a concentrations, were lower in 1978, particularly in the latter part of the summer, than in previous years (Fig. 22). Thus, less food material may have been available for larvae towards the end of the year. Other environmental factors that may have increased the mortality of larvae or decreased the success of oviposition cannot be discounted.

e) Spatial dispersion of populations

The parameter b of Taylor's power law (Taylor, 1961) is a measure of the degree of clumping in populations and is often fairly constant for a species (Elliott, 1971).

$$b = \frac{(\overline{x-\bar{x}})(\overline{y-\bar{y}})}{(\overline{x-\bar{x}})^2}$$

where $x = \log \bar{x}$ and $y = \log S^2$ for each sample. The parameter b is calculated from the regression line of $\log S^2$ on $\log \bar{x}$ for each taxon. The advantage of the method is that from b a common transformation can be applied to the original counts to normalise the frequency distribution of the counts, eliminate the dependence of the variance on the mean and ensure that the components of the variance are additive (Elliott, 1971).

Regression lines of $\log S^2$ on $\log \bar{x}$ were calculated for 12 chironomid taxa using data from all grab samples taken each month (Fig. 42 and Table 24). Similar regression lines were calculated for all taxa indicating similar contagious dispersion patterns. Ablabesmyia and Glyptotendipes showed the least contagious distributions. These taxa occurred in very low numbers in Rutland Water.

The appropriate transformation to apply to the original counts of these 12 chironomid taxa is x^p , where

$$p = 1 - b/2$$

Table 25 provides an accurate statement of the power law for each of the 12 taxa. Application of Taylor's power law model, as calculated for each taxon, enables standard parametric tests to be applied to the data.

Several indices of dispersion have been calculated to compare seasonal changes in dispersion of the five most abundant chironomid taxa in Rutland Water. The variance to mean ratio (Elliott, 1971) was used to test for agreement with a Poisson series:

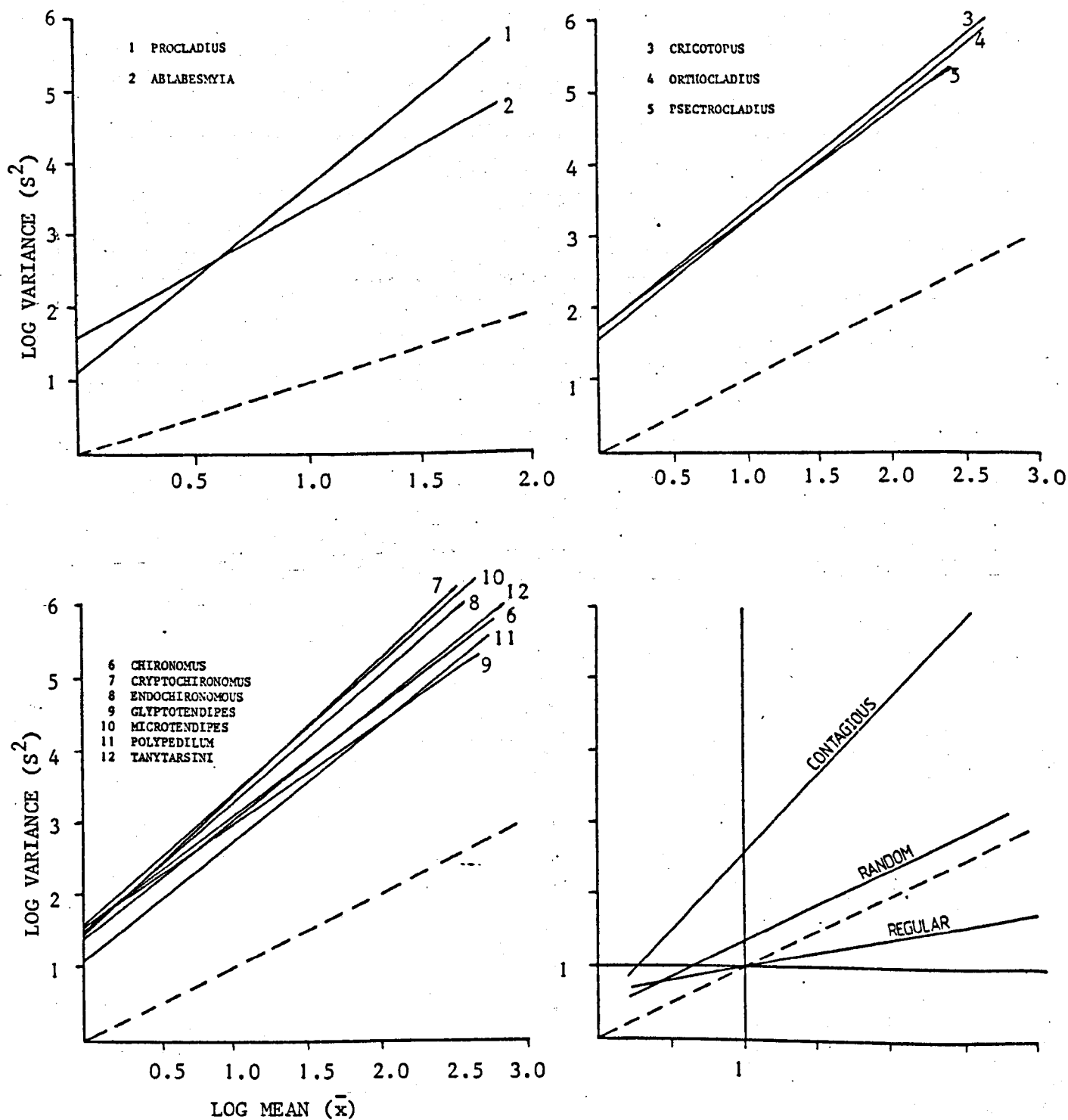


Fig. 42. Relationship between variance and mean of the population density of twelve chironomid taxa at Rutland Water. Equations for the regression lines are given in Table 24.

Table 24: Regression line parameters for log variance (S^2) on log mean (\bar{x}) of the population density for 12 chironomid taxa at Rutland Water. Each data pair is calculated from greater than 40 sampling units.

	Population Parameters		Number of Data Pairs	Correlation Coefficient
	a (slope)	b (intercept)		
Procladius	1.69	1.21	27	0.95
Ablabesmyia	1.78	1.64	18	0.94
Cricotopus	1.63	1.78	16	0.96
Orthocladius	1.53	1.78	11	0.97
Psectrocladius	1.68	1.62	21	0.91
Chironomus	1.56	1.58	27	0.96
Cryptochironomus	1.60	1.48	25	0.94
Endochironomus	1.47	1.53	18	0.96
Glyptotendipes	1.54	1.56	21	0.91
Microtendipes	1.43	1.60	24	0.92
Polypedilum	1.71	1.12	25	0.91
Tanytarsini	1.70	1.40	19	0.97

Table 25: Statement of the power law for 12 chironomid taxa at Rutland Water. δ^2 = variance, μ = arithmetic mean, p = power transformation to be applied to original counts.

Taxa	Statement of Power Law	Power Transformation (P)
Procladius	$\delta^2 = 48.59 \mu^{1.69}$	0.16
Ablabesmyia	$\delta^2 = 43.85 \mu^{1.78}$	0.11
Cricotopus	$\delta^2 = 60.39 \mu^{1.63}$	0.18
Psectrocladius	$\delta^2 = 41.89 \mu^{1.68}$	0.16
Orthocladius	$\delta^2 = 59.56 \mu^{1.53}$	0.23
Chironomus	$\delta^2 = 38.19 \mu^{1.56}$	0.22
Cryptochironomus	$\delta^2 = 30.04 \mu^{1.60}$	0.20
Endochironomus	$\delta^2 = 34.07 \mu^{1.47}$	0.26
Glyptotendipes	$\delta^2 = 36.49 \mu^{1.54}$	0.23
Microtendipes	$\delta^2 = 40.35 \mu^{1.43}$	0.29
Polypedilum	$\delta^2 = 13.32 \mu^{1.71}$	0.15
Tanytarsini	$\delta^2 = 25.05 \mu^{1.70}$	0.15

$$I = S^2 / \bar{x}$$

where I = coefficient of dispersion, S^2 = variance and \bar{x} = mean. The significance of the deviation from randomness was determined from the chi-square approximation (Elliott, op. cit.):

$$\chi^2 = S^2 / \bar{x} \quad (n-1)$$

with degrees of freedom $v = n-1$. Where the number of samples was large the standard normal deviate (Elliott, opt. cit.) was evaluated:

$$d = \sqrt{2\chi^2} - \sqrt{2v-1}$$

Indices of dispersion are influenced by the number of samples (n), the mean density (\bar{x}) and the total number of individuals ($\sum x$). They test the departure from randomness but are not efficient for the description of the degree of clumping of individuals. Green (1966) proposed an index that takes values between zero (randomness) and unity (maximum positive contagion) and is independent of n, \bar{x} and $\sum x$:

$$C_x = \frac{(S^2/\bar{x}) - 1}{\sum x - 1}$$

where \bar{x} = mean density per sample, S^2 = variance and $\sum x$ = total number of individuals.

Using combined data from all six transects Procladius (Table 26), Psectrocladius (Table 27), Chironomus (Table 28), Polypedilum (Table 29) and Tanytarsini (Table 30) showed highly contagious distributions, as indicated by all three indices, in most months throughout 1978. Populations showed a tendency to become more contagiously distributed when the population declined. Using Green's coefficient this was most pronounced for Procladius in September and October (Table 26), Chironomus in August and September (Table 28) and Polypedilum in August (Table 29).

Table 26: Dispersion of Procladius recorded in the 1978 samples. Contagious distribution is indicated if $I > 1$; $d > 1.96$ and $Cx > 0$.

Date 1978	No. of Samples	Mean popn. density m^{-2} \pm Standard error ($\bar{x} \pm S.E.$)	Variance (S^2)	Dispersion Index (I)	Standard Normal Deviate (d)	Green's coefficient (Cx)
J	46	158.8 \pm 27.4	34631	218.0	130.7	0.030
F	46	133.9 \pm 28.5	37426	279.5	149.2	0.045
M	46	79.4 \pm 17.5	14165	178.4	117.3	0.049
A	46	133.9 \pm 25.0	28821	215.2	129.8	0.035
M	46	98.5 \pm 23.1	24539	249.1	140.3	0.055
J	46	127.2 \pm 25.5	29877	234.9	136.0	0.040
J	46	110.0 \pm 29.2	39215	356.5	169.7	0.070
A	46	33.5 \pm 8.9	3629.8	108.4	89.4	0.070
S	46	13.4 \pm 5.3	1279.4	95.5	83.3	0.154
O	46	44.0 \pm 14.2	9292.8	211.2	128.5	0.104
N	46	53.6 \pm 11.4	5929.6	110.6	90.4	0.044
D	46	94.7 \pm 21.9	22024.6	232.6	135.3	0.053

Table 27: Dispersion of Psectrocladius recorded in the 1978 samples. Contagious distribution is indicated if $I > 1$; $d > 1.96$ and $Cx > 0$.

Date 1978	No. of Samples	Mean popn. density m^{-2} \pm Standard error ($\bar{x} \pm S.E.$)	Variance (s^2)	Dispersion Index (I)	Standard Normal Deviate (d)	Green's coefficient (Cx)
J	46	14.3 \pm 6.4	1897.7	132.7	99.9	0.200
F	46	6.7 \pm 4.1	771.6	115.2	92.4	0.372
M	46	12.4 \pm 7.2	2380.3	192.0	122.1	0.335
A	46	12.4 \pm 5.1	1175.6	94.8	83.0	0.164
M	46	-	-	-	-	-
J	46	47.8 \pm 25.2	29154.1	609.9	224.9	0.277
J	46	9.6 \pm 4.1	766.9	79.9	75.4	0.180
A	46	-	-	-	-	-
S	46	-	-	-	-	-
O	46	-	-	-	-	-
N	46	-	-	-	-	-
D	46	-	-	-	-	-

Table 28: Dispersion of Chironomus recorded in the 1978 samples. Contagious distribution is indicated if $I > 1$; $d > 1.96$ and $Cx > 0$.

Date 1978	No. of Samples	Mean popn. density m^{-2} ± Standard error ($\bar{x} \pm S.E.$)	Variance (s^2)	Dispersion Index (I)	Standard Normal Deviate (d)	Green's coefficient (Cx)
J	46	272.6 ± 46.5	99520.7	365.1	171.9	0.029
F	46	244.9 ± 55.7	142803.8	583.1	219.7	0.052
M	46	146.3 ± 29.7	40703.7	278.2	148.8	0.041
A	46	230.5 ± 56.3	146205.4	634.3	229.5	0.060
M	46	278.3 ± 111.4	570565.4	2050.2	420.2	0.160
J	46	79.4 ± 20.5	19241.2	242.3	138.3	0.066
J	46	21.0 ± 4.9	1096.1	52.2	59.1	0.053
A	46	1.9 ± 1.9	168.3	88.6	79.9	1.007
S	46	1.0 ± 1.0	42.1	42.1	52.2	0.956
O	46	11.5 ± 4.4	897.9	78.1	74.4	0.146
N	46	24.9 ± 8.7	3497.9	140.5	103.0	0.122
D	46	3.8 ± 2.3	243.2	64.0	66.5	0.360

Table 29: Dispersion of Polypedilum recorded in the 1978 samples. Contagious distribution is indicated if $I > 1$; $d > 1.96$ and $Cx > 0$.

Date 1978	No. of Samples	Mean popn. density m^{-2} + Standard error ($\bar{x} \pm S.E.$)	Variance (S^2)	Dispersion Index (I)	Standard Normal Deviate (d)	Green's coefficient (Cx)
J	46	455.3 \pm 97.5	436866.4	959.5	284.5	0.046
F	46	282.2 \pm 62.8	181259.2	642.3	231.0	0.049
M	46	181.7 \pm 32.6	48753.5	268.3	146.0	0.032
A	46	261.1 \pm 61.5	174102.5	666.8	235.6	0.055
M	46	101.4 \pm 18.9	16509.3	162.8	111.6	0.035
J	46	20.1 \pm 4.7	1007.3	50.1	57.7	0.053
J	46	9.6 \pm 3.0	422.7	44.0	53.5	0.098
A	46	6.7 \pm 3.3	513.5	76.6	73.6	0.246
S	46	19.1 \pm 7.9	2895.6	151.6	107.4	0.171
O	46	43.0 \pm 10.6	5204.8	121.0	95.0	0.061
N	46	78.4 \pm 29.0	38798.5	494.9	201.6	0.137
D	46	41.1 \pm 9.6	4250.8	103.4	87.1	0.054

Table 30: Dispersion of Tanytarsini recorded in the 1978 samples. Contagious distribution is indicated if $I > 1$; $d > 1.96$ and $Cx > 0$.

Date 1978	No. of samples	Mean popn. density m^{-2} + Standard error ($\bar{x} \pm S.E.$)	Variance (S^2)	Dispersion Index (I)	Standard Normal Deviate (d)	Green's coefficient (Cx)
J	46	211.4 \pm 49.7	113718.0	537.9	210.6	0.055
F	46	225.7 \pm 48.0	105801.0	468.8	196.0	0.045
M	46	279.3 \pm 53.0	129171.4	462.5	194.6	0.036
A	46	485.0 \pm 100.8	467263.4	963.4	285.1	0.043
M	46	243.9 \pm 43.5	87137.8	357.3	169.9	0.032
J	46	179.8 \pm 91.3	383743.3	2134.3	428.9	0.258
J	46	96.6 \pm 43.9	88679.1	918.0	278.0	0.207
A	46	69.8 \pm 22.1	22507.2	322.5	161.0	0.100
S	46	14.3 \pm 5.3	1295.3	90.6	80.9	0.121
O	46	11.5 \pm 4.6	983.9	85.6	78.4	0.161
N	46	139.7 \pm 63.9	188291.4	1347.8	338.9	0.210
D	46	204.7 \pm 92.9	396769.6	1938.3	408.3	0.206

Two hypotheses may be forwarded to account for these contagious distributions. Firstly, larvae of certain species may tend to behaviourally aggregate. No data are available from this study or the literature to test this hypothesis. Secondly, larvae tend to aggregate as a result of habitat heterogeneity. For example, a number of environmental parameters are known to vary with water depth (e.g. light, temperature, oxygen concentration); substrate variations are also known to occur within the reservoir.

The spatial dispersion patterns within different depth zones were investigated by combining data from all six transects and dividing the sampling units into four depth zones. Green's coefficient was calculated for five taxa and for three selected months of varying population density in 1978. This index was selected due to its independence of variation in the number of sampling units. With only one exception (Procladius, 6-10m), the lower population densities in September 1978 showed a higher degree of contagion than the higher population densities in March, for all five taxa and all four depth zones (Table 31). Using the non-parametric Spearman's rank correlation coefficient (Elliott, 1971) all five taxa showed a significant ($p < 0.05$) correlation between population density and the value of Green's coefficient. However, apart from trends associated with the decreasing population density no clear relationship between Green's coefficient and water depth can be seen. This analysis would be improved by the use of larger numbers of samples taken within narrower depth zones.

In order to assess the spatial dispersion patterns of chironomid larvae within one substrate type 30 grab samples were collected in June 1978 from a small area, approximately 8 m² and 5 m deep. The dispersal index for the three taxa recorded from this site (Table 32) are lower, i.e. more randomly distributed, than the corresponding values for the same taxa, month and depth zone calculated after combining samples from different parts of

Table 31: Green's coefficient of dispersion for five taxa in four depth zones. Sampling units taken from all transects (n = sample number, \bar{x} = mean population density and C_x = Green's coefficient)

	March 1978				June 1978				September 1978			
	n	\bar{x}	C_x	n	\bar{x}	C_x	n	\bar{x}	n	\bar{x}	C_x	C_x
Procladius	0-5m	25	420	0.123	19	270	0.355	20	49	0.191		
	6-10m	12	748	0.182	18	646	0.069	19	107	0.174		
	11-15m	18	142	0.071	14	506	0.097	12	41	0.821		
	16+m	11	48	0.281	15	59	0.104	15	21	0.336		
Psectrocladius	0-5m	25	393	0.198	19	1074	0.299	20	40	0.421		
	6-10m	12	31	0.198	18	2	0.887	19	0	-		
	11-15m	18	2	0.860	14	0	-	12	0	-		
	16+m	11	4	1.000	15	62	0.994	15	0	-		
Chironomus	0-5m	25	202	0.166	19	49	0.240	20	53	0.379		
	6-10m	12	188	0.100	18	88	0.099	19	8	0.340		
	11-15m	18	156	0.091	14	126	0.173	12	4	0.907		
	16+m	11	204	0.176	15	18	0.335	15	0	-		
Polypedilum	0-5m	25	471	0.100	19	56	0.376	20	12	0.548		
	6-10m	12	171	0.063	18	16	0.341	19	20	0.287		
	11-15m	18	126	0.116	14	45	0.120	12	6	0.493		
	16+m	11	284	0.074	15	26	0.181	15	35	0.302		
Tanytarsini	0-5m	25	1084	0.209	19	2385	0.295	20	14	0.279		
	6-10m	12	778	0.161	18	35	0.161	19	126	0.239		
	11-15m	18	376	0.083	14	267	0.769	12	33	0.271		
	16+m	11	228	0.159	15	3	0.977	15	21	0.205		

Table 32: Green's coefficient of dispersion for the dominant taxa occurring at one site 8m deep in June 1978.

	Number of Sampling Units	Mean Population Density	Green's Coefficient
	(n)	(\bar{x})	(Cx)
Procladius	30	255	0.049
Chironomus	30	44	0.083
Tanytarsini	30	18	0.076

the reservoir (Table 31). The corresponding mean populations are also lower in each case. This contradicts the general trend of larvae showing more highly contagious distributions at lower population densities when calculated from combined samples (Table 31). It is thus possible that at low population densities combined samples from different parts of the reservoir indicate contagious distributions due mainly to the effects of substrate variation and that populations within one substrate type are more randomly distributed.

(f) Spatial variation of chironomid fauna within the reservoir

In order to compare the spatial variation of the chironomid fauna throughout the reservoir each transect has been treated as one sampling station, composed of 10 or 12 sampling units (grab samples) per sampling date.

Taking the sampling period as a whole, the largest populations were recorded from the two transects at the western end of the reservoir (Fig. 43). At all sites the Chironominae represented more than 50% of the total chironomid fauna. The proportion of Tanypodinae was comparatively constant between the sites and varied from 13% at the south-arm transect to 27% at the second south-arm transect. The proportion of Orthocladiinae was low at the dam and tower transects. The tower transect was expected to have a lower proportion of Orthocladiinae larvae as unlike the other transects it runs from the shore to a deep water point at the limnological tower (Fig. 16). Thus, the shallow water Orthocladiinae larvae do not occur at both ends of the transect. The largest proportion of Orthocladiinae larvae was recorded at the second north-arm transect (Fig. 43).

The population densities of the three major subfamilies of the Chironomidae, for each transect, in each month, are shown in Figure 44. Throughout the study period the tower, dam, south-arm and north-arm transects all showed similar population changes and densities.

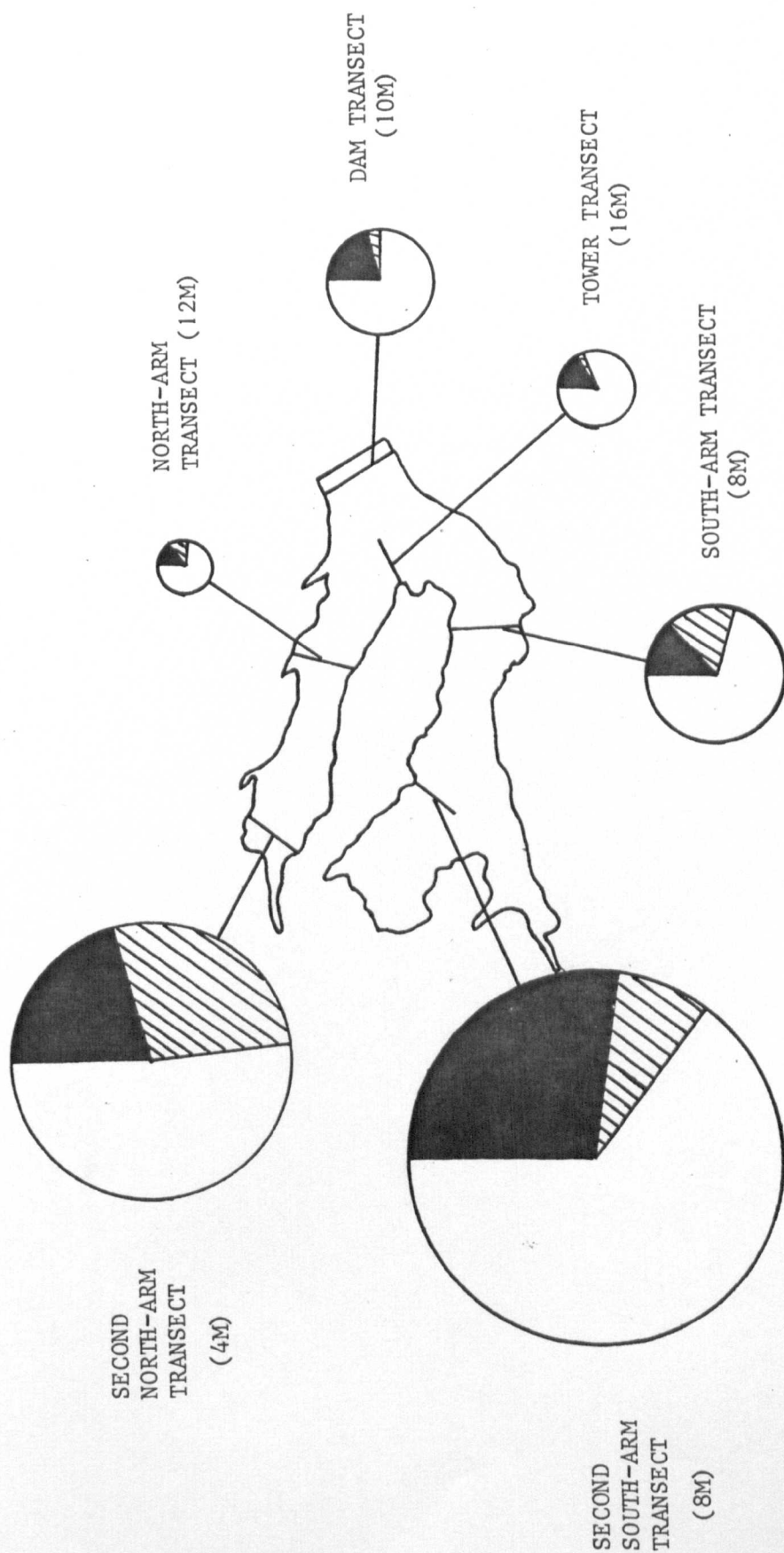


Fig. 43. Composition of chironomid subfamilies and abundance (m^2 proportional to circle radius) at each transect, calculated from all monthly samples. Mean depth of transect (for April 1978) is given in brackets. Black - Tanypodinae; cross-hatched - Orthocladinae; white - Chironominae

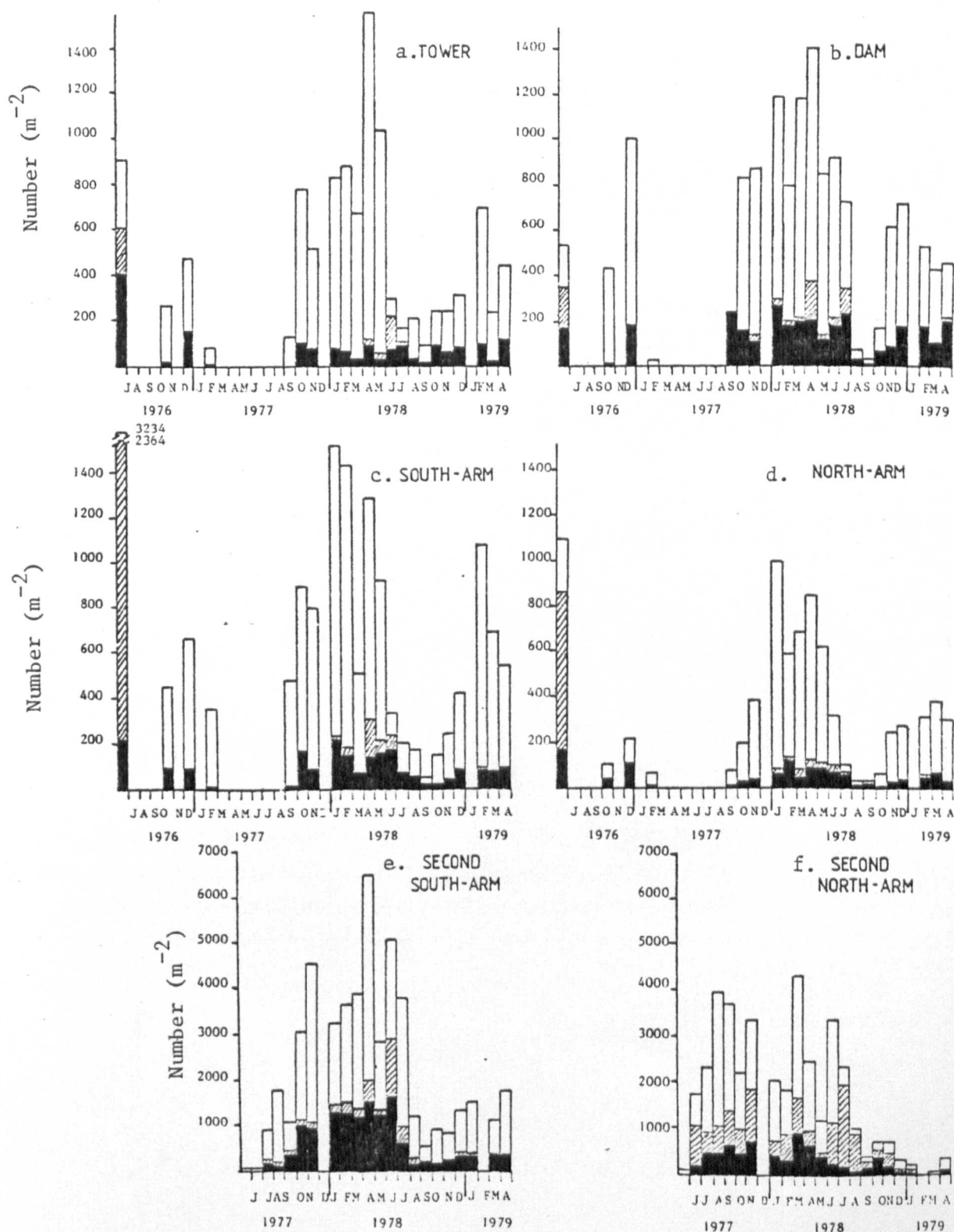


Fig. 44. Changes in abundance of chironomid subfamilies at each transect. Black - Tanypodinae; crosshatched - Orthocladiinae; white - Chironominae. Note change of scale for second south-arm and second north-arm transects.

The maximum population density recorded in the tower transect occurred in April 1978 and the minimum in September 1978 after the summer emergence period. This transect runs from the shore to the limnological tower located in deep water in the central basin (Fig. 16) and the fauna might, therefore, be affected by stratification. Although a thermocline began to form in May 1978, it was later disturbed, possibly by wind action (Fig. 20), so that the effects of stratification on the fauna cannot be ascertained.

The dam transect had the highest overwintering population in 1976-77 of the four transects sampled at that time. As in the tower transect the maximum population density occurred in April 1978 (Fig. 44). Generally the population density of Tanypodiinae was higher in the first six months of 1978 than in the tower, south-arm or north-arm transects. After the decline in larval density at the end of the summer the population increased more rapidly to higher densities at the end of the year than the other transects. This may be the result of successful oviposition of females in this region of the reservoir resulting in a high density of larvae or the migration of larvae to this area due to unfavourable conditions elsewhere.

The south-arm transect had exceptionally high densities of Orthocladiinae larvae in July 1976 (Fig. 44). This was discussed in section d, Chapter 5. In contrast to the dam and tower transects the higher population densities occurred at the beginning of 1978 and these declined gradually to a minimum of 5lm^{-2} in September 1978. Populations increased at the end of the year but not to the same densities as recorded in 1977. The generally lower population densities recorded at the end of 1978 and beginning of 1979 may, compared to the previous winter period, be the result of climatic differences and these have been discussed in section d.

The north-arm transect also had a high proportion of Orthoclaadiinae larvae in July 1976 (Fig. 44). Generally the density of larvae of all three subfamilies was lower in this transect than in the other five transects. The lowest population densities (37m^{-2} based on 12 sampling units along the transect) for the whole reservoir were recorded in September 1978 in the north-arm transect after the summer emergence period.

Sampling of the two transects located at the western end of the reservoir (second south-arm and second north-arm) began in May 1977. The other four transects were not sampled at this time. Very low populations were recorded in the second south-arm transect in May and June 1977, and in the second north-arm transect in May 1977 (Fig. 44). Populations increased rapidly in the two transects to $1,763\text{m}^{-2}$ (based on 10 grab samples) in the second south-arm transect and to $3,952\text{m}^{-2}$ in the second north-arm transect by August 1977. In the second south-arm transect the maximum population density was recorded in April 1978. A much lower population density was recorded the following month mainly as a result of the decrease in number of Chironomini larvae, possibly due to emergence (Fig. 44).

Lower population densities were recorded in the first six months of 1978 in the second north-arm transect compared to the second south-arm transect. Throughout most of the sampling period the number of Orthoclaadiinae larvae was, however, higher. This is related to the comparatively shallow mean depth of this transect (Fig. 43). Large beds of filamentous algae developed, a suitable habitat for these larvae, which did not occur to the same extent in the other transects. Unlike the other five transects, population densities remained low in the first few months of 1979.

This initial comparison of the six transects (Fig. 44) reveals that the closest similarities in temporal changes and

population densities occur between the north-arm and dam transects; the south-arm and tower transects; and the second north-arm and second south-arm transects. The transects were compared statistically using Kendall's rank correlation coefficient (Klecka, Nie and Hadlai Hull, 1975):-

$$r = \frac{2S}{n(n-1)}$$

where r = Kendall's coefficient, n = number of variable pairs, S = Kendall's ranking statistic. This is a non-parametric test and, therefore, the data were not transformed. Correlation coefficients were calculated from variable pairs, number of Chironomidae per square metre, from all six transects, monthly from September 1977 to April 1979, except December 1977 and January 1978 when not all transects were sampled (Table 5).

The north-arm transect showed significant correlations with three other transects, tower ($P < 0.01$), south-arm ($P < 0.01$) and the second south-arm ($P < 0.05$) (Table 33). The tower transect also showed a significant correlation ($P < 0.05$) with the second south-arm transect. Chironomid populations from the dam and second north-arm transects did not correlate significantly with any other transects.

Kendall's correlation coefficient only compares changes in the total chironomid fauna between each pair of transects. In order to compare the abundance of the dominant species or taxa for each pair of transects, Raabe's coefficient (Raabe, 1952) was calculated:-

$$R = \sum \min(a, b, c \dots n)$$

where R = Raabe's coefficient, a = percentage of species 'a' common to both transects, b = percentage of species 'b' common to both transects, n = total number of species. The coefficient ranges from 0 to 100, with identical species assemblages in two stations giving a coefficient of 100. Coefficients were calculated

Table 33: Kendall's rank correlation coefficients of numbers per metre square from the six transects, September 1977 to April 1979

Variables									
North-Arm	1								
Dam	0.304	1							
Tower	**0.498	0.193	1						
South-Arm	**0.503	8.118	0.362	1					
Second South-Arm	*0.415	0.155	0.435	0.221	1				
Second North-Arm	4.445	-0.185	9.594	-0.176	0.294	1			
Against Variable	North-Arm	Dam	Tower	South-Arm	Second South-Arm	Second North-Arm			

* Significant at 5% level

** Significant at 1% level

for each pair of transects and this was repeated monthly for the first eight months of 1978. This enables temporal differences in the species assemblages at each transect to be compared and the time span covers the maximum range of population densities recorded during the year.

Matrices of Raabe's coefficients for each month are given in Table 34 and the major components of the matrices are represented graphically as single linkage clusters in Figure 45. The disadvantage with this graphical representation is that a member may be admitted to a cluster with a high level of affinity to only one other member of that cluster. Reference to the full matrix (Table 34) will determine if that is the case.

Generally at the high population densities of the winter and spring (Fig. 44) all six transects become clustered at high coefficients, > 65 for Raabe's coefficient (Fig. 45). At lower population densities in the summer months (Fig. 44) the transects become more dissimilar with some members only entering the clusters at low coefficients (Fig. 45). In order to examine the relationships between transects in terms of the chironomid species composition and abundance each month will be considered separately.

January: In January 1978 the six transects could be roughly divided into two groups, (T, NA, SA) and (D, 2SA, 2NA), on the basis of the cluster analysis (Fig. 45). The first group of transects were associated with each other mainly because they all had high densities of Chironomus and Polypedilum larvae (Appendix C). The second group of transects were associated because of their high population densities of Procladius and Tanytarsini larvae. A number of hypotheses may be advanced to explain these results. For example, differences in environmental factors may produce niches suitable to particular groups of larvae; alternatively, environmental factors may produce different rates of growth and consequently different periods of emergence.

Table 34: Raabe's coefficients of similarity between each transect during the first eight months of 1978.

○ = highest coefficient in matrices; NA = north-arm, D = dam, T = tower, SA = south-arm,

2SA = second south-arm and 2NA = second north-arm transects.

	NA	D	T	SA	2SA	2NA	NA	D	T	SA	2SA	2NA
NA	XX	56	74	76	48	35	XX	86	64	65	73	66
D	XX	XX	67	73	79	71		XX	57	60	70	68
T		XX	XX	76	51	38			XX	91	50	39
SA				XX	67	54				XX	52	41
2SA	JANUARY			XX	XX	68	FEBRUARY			XX	XX	72
2NA						XX						XX
NA	XX	62	78	83	69	50	XX	66	79	75	66	56
D	XX	XX	68	65	70	77		XX	55	87	81	77
T		XX	XX	87	70	52			XX	64	57	46
SA				XX	67	48				XX	81	69
2SA	MARCH			XX	XX	76	APRIL			XX	XX	85
2NA						XX						XX
NA	XX	66	29	68	61	65	XX	56	45	54	56	43
D	XX	XX	29	81	67	68		XX	35	42	65	76
T		XX	XX	50	19	23			XX	59	53	35
SA				XX	59	66				XX	59	35
2SA	MAY			XX	XX	83	JUNE			XX	XX	71
2NA						XX						XX
NA	XX	57	81	63	43	24	XX	50	41	63	41	19
D	XX	XX	49	47	68	34		XX	60	77	59	19
T		XX	XX	62	43	26			XX	72	83	19
SA				XX	38	21				XX	70	21
2SA	JULY				XX	40	AUGUST			XX	XX	31
2NA						XX						XX

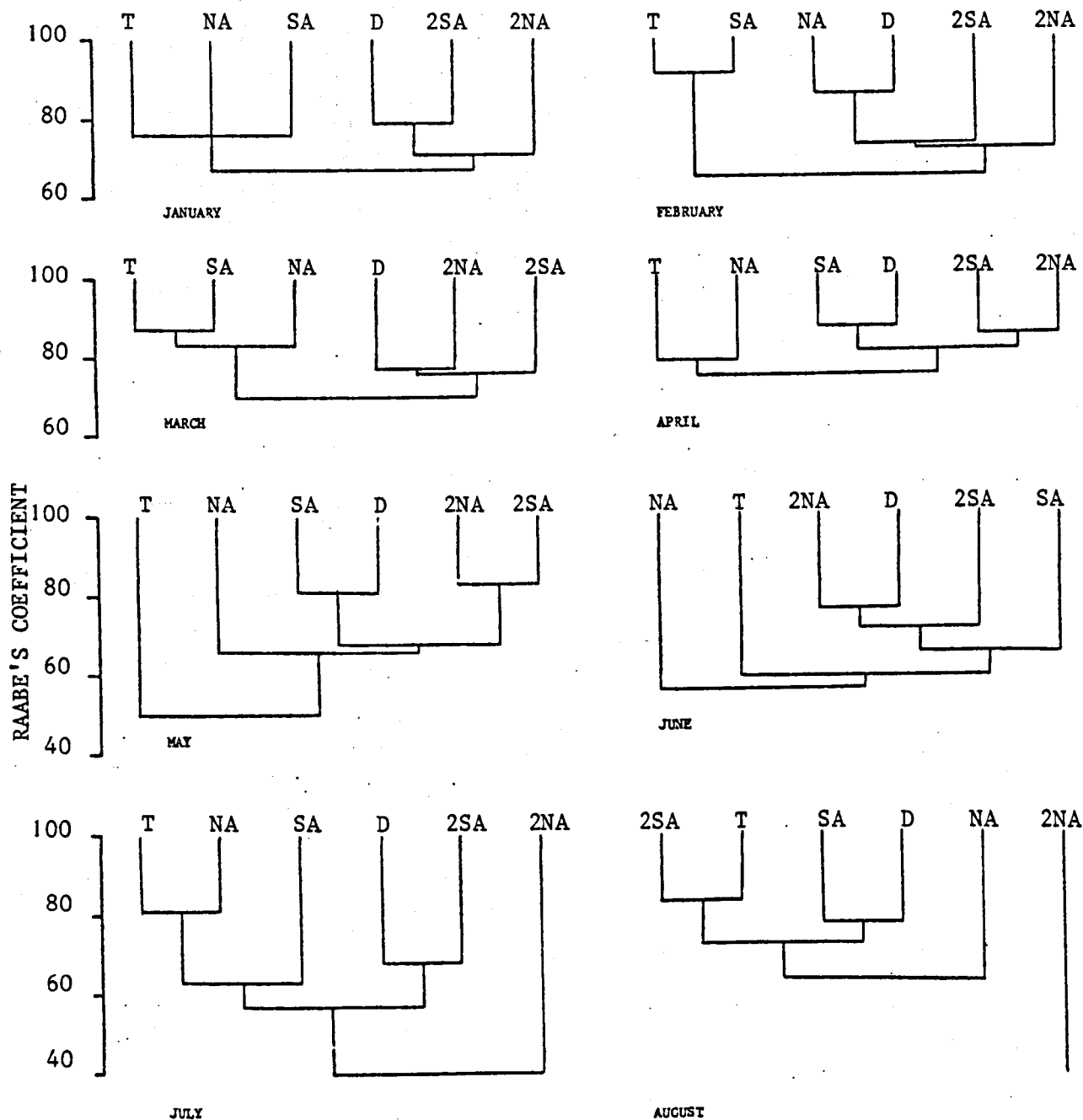


Fig. 45. Dendrograms of single linkage clusters between transect sites, based on Table 34. NA - north-arm; D - dam; T - tower; SA - south-arm; 2SA - second south-arm; 2NA - second north-arm transect.

February: The main change from January to February was that the north-arm transect changed groups; which then became (T, SA) and (NA, D, 2SA, 2NA) (Fig. 45). This was a direct result of the decline in numbers of Polypedilum larvae, from 623m^{-2} in January to 70m^{-2} in February, in the north-arm transect. This did not occur in either the tower or south-arm transects. The decline in the numbers of Polypedilum may have been due to mortality, for example, by predation or some abiotic factor or due to the physical movement of larvae away from the site, for example by migration or emergence.

March: In March the north-arm transect changed back to form the original groupings and this was the result of an increase in numbers of Polypedilum larvae. This suggests that errors in sampling may have resulted in the low recorded numbers of Polypedilum larvae in the north-arm transect in February. The second group of transects (D, 2SA, 2NA) were still dominated by Tanytarsini larvae.

April: The main change in April was due to an increase in the density of Procladius, Cricotopus and Tanytarsini larvae in the south-arm transect which transferred it to the second group of transects. The increase in numbers of these taxa did not occur in either the tower or north-arm transects. In this second group of transects the south-arm and dam were closely associated and Procladius, Cricotopus, Chironomus, Polypedilum and Tanytarsini dominated the fauna. Similarly the second south-arm and second north-arm transects were associated and Procladius, Psectrocladius, Chironomus, Endochironomus, Polypedilum and Tanytarsini dominated their fauna.

May: In May the second cluster of transects (SA, D, 2SA, 2NA) remained almost the same. The first group (T, NA), however, became dissociated from each other and the second cluster of transects. This was the result of more complex changes in the chironomid fauna than had previously been recorded. In the north-arm

transect Chironomus larvae declined in numbers whilst Endochironomus increased. In the tower transect Polypedilum and Tanytarsini larvae decreased in number whilst Chironomus increased.

June: In June the picture remained similar to May although there were some slight changes in the similarity coefficients in the second group of transects (2NA, D, 2SA, SA).

July and August: In these two months the relationships between the transects were changing. This is the result of very small but numerous changes in numbers and species composition of the fauna in each of the transects.

The changes in similarity coefficients of transects in consecutive months reflect the dynamic nature of the populations with species composition and densities changing from site to site. No attempt has been made in this study to determine the factors causing these changes. Several possibilities exist, spatial variation in emergence of species, migration of larvae, differing levels of predation, variation in abiotic factors. It is thought likely that during the late spring and summer different emergence patterns may be the main factor. This may come about due to environmental variations such as substrate type, water temperature and food supply that produce different rates of growth and hence different times of emergence. There are other physical differences between transects, such as mean water depth, which result in differences in the proportions of certain groups.

(g) Depth distributions

The distribution of chironomid species with water depth was investigated utilising data from the second north-arm and second south-arm transects (see Fig. 16 for locations, profiles and maximum depths). The number of larvae in each grab sample was converted to numbers per square metre and the results plotted against depth recorded at the time of sampling. The calculated

depths of grab samples collected from the other four transects were not considered to be sufficiently accurate to warrant inclusion in the data presented here. However, data on the maximum depths at which species were recorded at Rutland Water have been given in the text.

Tanypodinae

Larvae of the genus Procladius, composed mainly of P. choreus, occurred in relatively large numbers down to 13m (Fig. 46). Populations showed some decline in numbers below 14m in the other transects although larvae (maximum population density 400m^{-2}) were recorded at the maximum depths sampled, approximately 25m. P. choreus has been found to have a wide depth distribution in other lakes and reservoirs. In Llyn Tegid, Hunt and Jones (1972) recorded P. choreus down to 20m and the maximum number found at this depth in July was 40m^{-2} . Mundie (1957) also found P. choreus at all depths in Kempton Park East reservoir. Miller (1941) suggested that the wide depth distribution in the Tanypodinae in general is related to their carnivorous diet and free living nature enabling them to occur in deeper water than herbivorous species. A number of other workers have commented on the predatory and free living nature of P. choreus (Johannsen, 1937; Bryce, 1960; Kajak and Dusoge, 1970). Barker and McLachlan (1979) present evidence that the Tanypodinae are primarily predators but in adverse conditions will utilise a range of food items, particularly detritus. Tanypod larvae containing only algae in their guts have been found by Armitage (1968) and Luferov (1956).

Ablabesmyia larvae, mainly A. monilis, were not found at depths greater than 8m, and the highest population density occurred in water less than 2m deep (Fig. 47). A. monilis has been recorded from many different habitats in lakes although little is known of its ecology (Sandberg, 1969). A similar depth distribution with high densities occurring between 1 and 2m deep was observed by Mundie (1957). He also recorded a few individuals

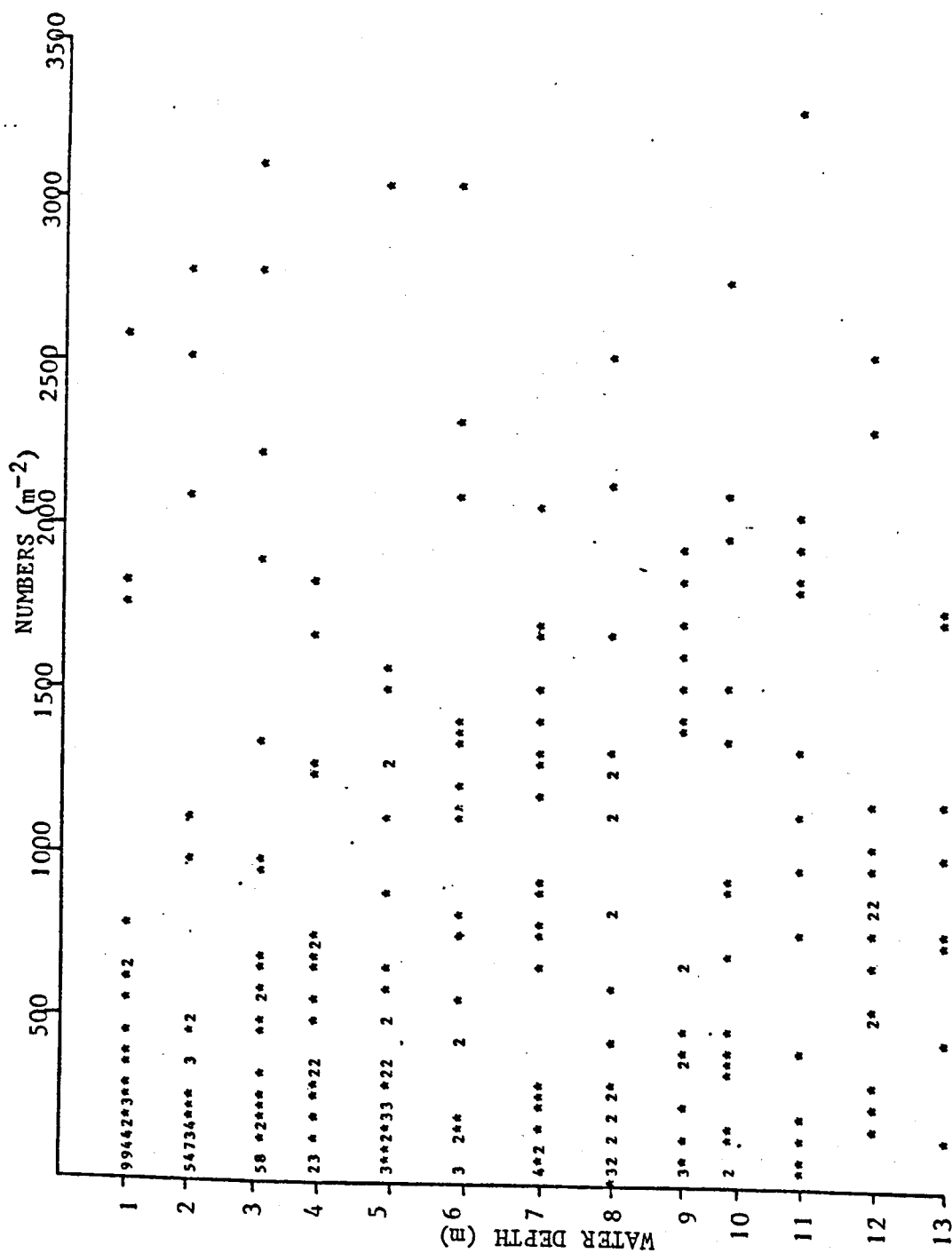


Fig. 46. Depth distribution of Procladius larvae based on grab samples collected from the second north-arm and second south-arm transects throughout the study.

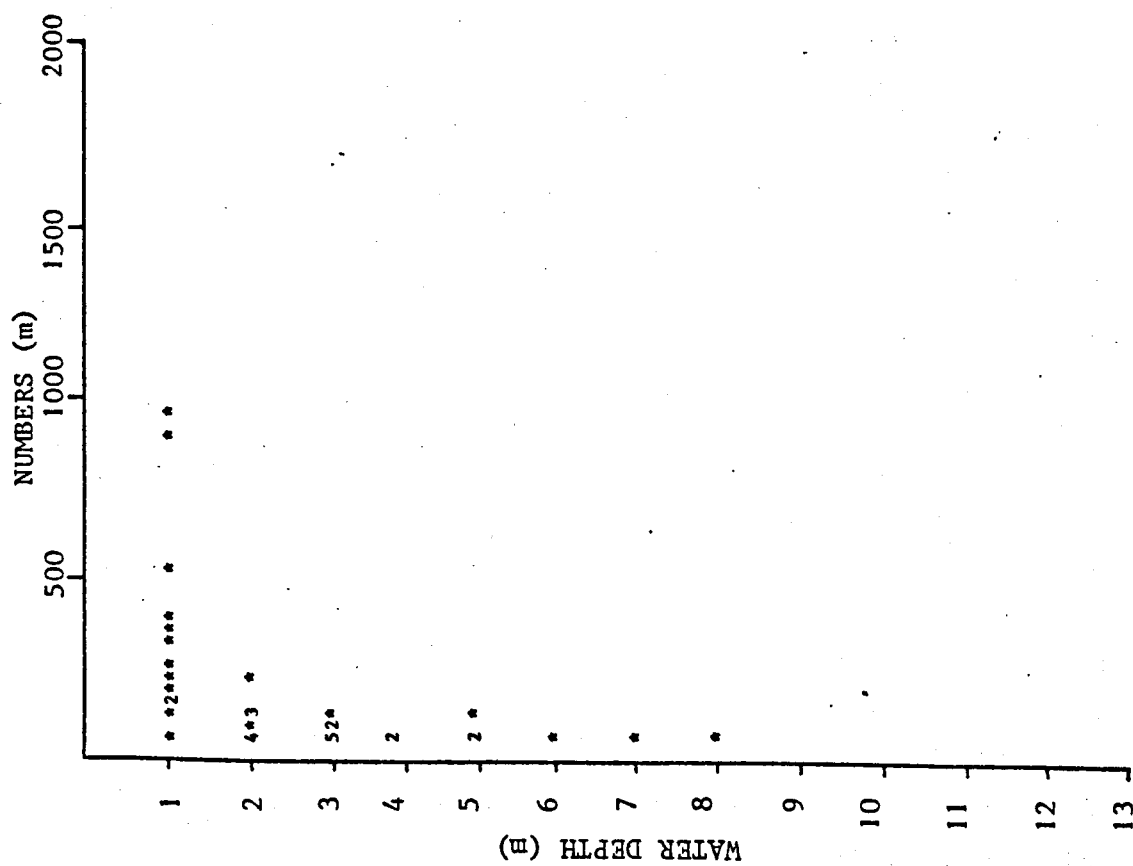


Fig. 47. Depth distribution of *Ablabesmyia* larvae based on grab samples collected from the second north-arm and second south-arm transects throughout the study.

at 9m and suggests that it may occur in the profundal zone of eutrophic lakes. The maximum depth of 8m recorded at Rutland Water suggests that this is probably the limit of its distribution.

Orthocladiinae

In general the Orthocladiinae are phytophilous, abundant in the littoral zone of lakes and reservoirs and also occur in many lotic habitats (Thienemann, 1954). Five species of Cricotopus were recorded in Rutland Water and almost all the larvae were found in water less than 3m deep (Fig. 48). A few isolated individuals were found at depths down to 16m. Miller (1941) recorded C. bicinctus at 7m in Costello Lake but generally the larvae of most species seem to be confined to the littoral zone where they build tubes or loose mats on aquatic macrophytes and other substrates (Lehman, 1971; Pankratova, 1968). At Rutland Water Cricotopus larvae were very numerous on dense mats of algae, mainly Cladophora sp. A similar observation was made by Mundie (1957) who also observed that breaking-up of the algal mat, by wave action for example, reduced the populations of these larvae. Mackey (1976) states that C. bicinctus group, and probably other species of Orthocladiinae, are only temporary tube dwellers. The larvae build a tube but later vacate it and build another one. Davies (1973) records several genera of Orthocladiinae in the plankton. It is possible that these planktonic larvae are carried by water currents and occasionally deposited in deep water. This may account for the specimens found in deep water grab samples at Rutland Water.

Four species of Orthocladius larvae were recorded at Rutland Water and were concentrated in water less than 4m deep (Fig. 49). A number of individuals were found in the plankton by Davies (1973) and again passive transport by water currents may account for their presence in deep water. It is also possible that the larvae found in deep water at Rutland Water were a different species to those found in the shallow water. Little is known about the ecology

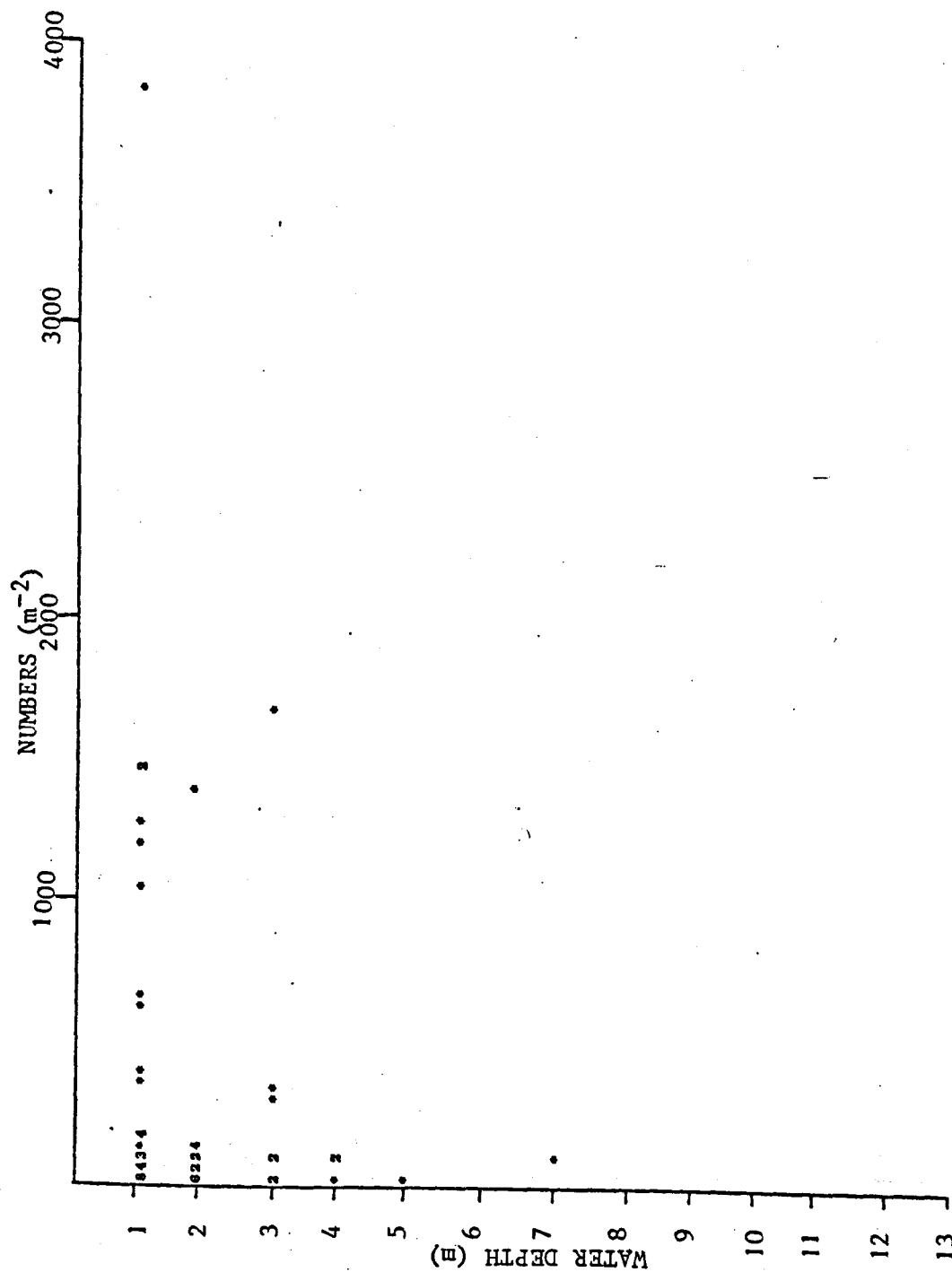


Fig. 48. Depth distribution of *Cricotopus* larvae based on grab samples collected from the second north-arm and second south-arm transects throughout the study.

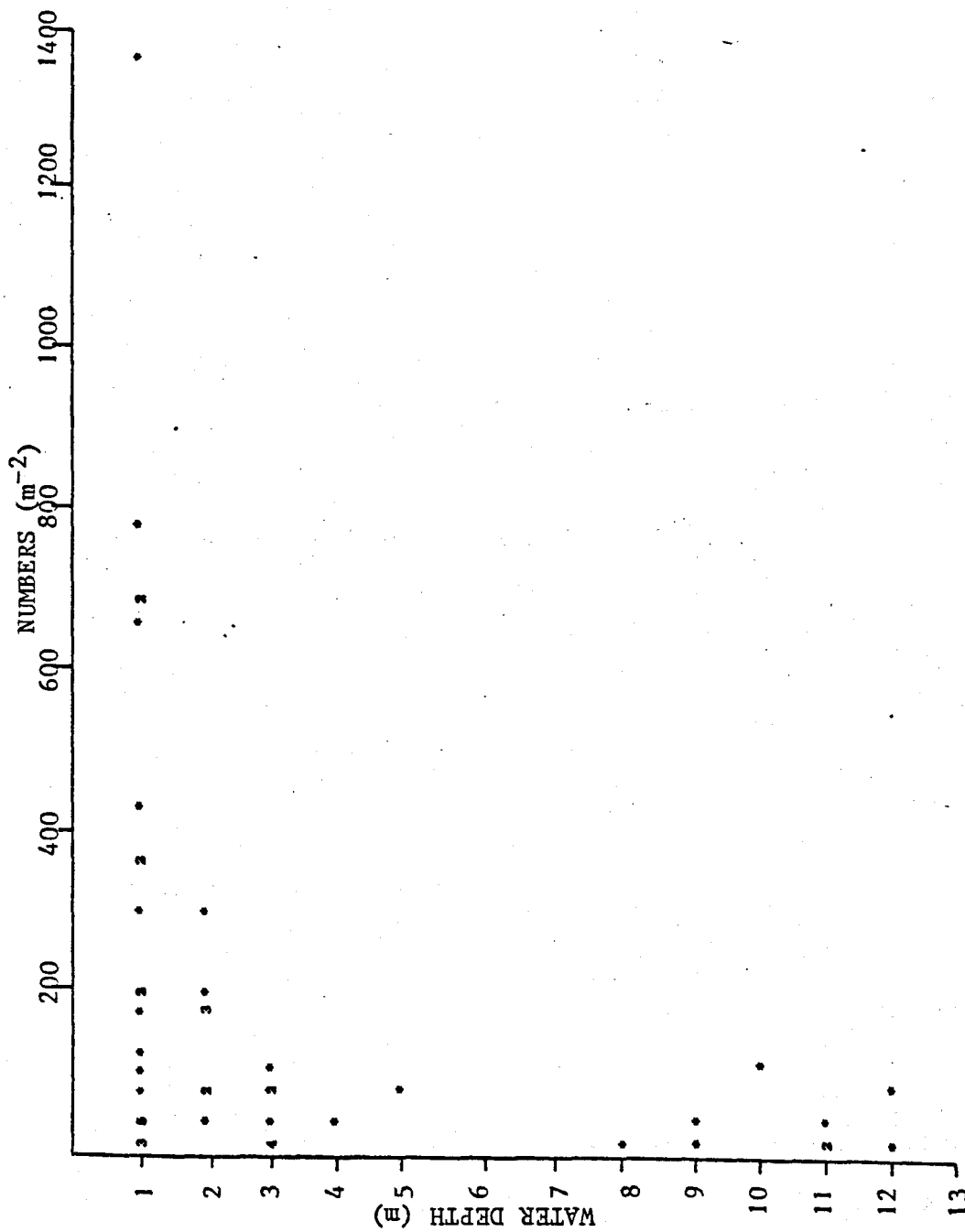


Fig. 49. Depth distribution of *Orthocladus* larvae based on grab samples collected from the second north-arm and second south-arm transects throughout the study.

of individual species of Orthocladius as the larvae are difficult to separate.

Psectrocladius larvae showed a general decline in numbers with increasing depth (Fig. 50). Low population densities of larvae were recorded continuously down to 20m. Mundie (1957) recorded P. limbatellus larvae down to 7m although as at Rutland Water the majority were confined to 0-3m. Little is known about the feeding habits of Psectrocladius but Mundie (op. cit.) suggests that it feeds on Cladophora and epiphytic algae.

Chironominae

Chironomus plumosus is a typical profundal species of eutrophic lakes (Humphries, 1938; Brundin, 1949). In Rutland Water Chironomus larvae occurred at all depths down to 13m although the highest population densities were found between 0 and 4m (Fig. 51). Population densities up to 700m^{-2} were recorded from the deepest parts of the reservoir sampled (tower transect), approximately 25m. This is in contrast to the findings by Mundie (1957) where C. plumosus was absent from the 1-3m depth zone for most of the year. Mundie suggested that shallow substrate may have been the cause of this.

Cryptochironomus larvae were found down to 13m, the maximum depth sampled in the second south-arm and second north-arm transects (Fig. 52). As with Chironomus the highest population densities were recorded in shallow water, 2m. Two species were separated but not identified. Mundie (1957) recorded five species of Cryptochironomus in Kempton Park East reservoir although in insufficient numbers to determine their depth distributions. Hunt and Jones (1972) found Cryptochironomus 'defectus' group, one of the groups recorded at Rutland Water, regularly down to 20m in Llyn Celyn. Occasional specimens were found down to 40m.

Endochironomus albipennis larvae showed a peak in population density at 4m (Fig. 53). Larvae were recorded down to 23m in the

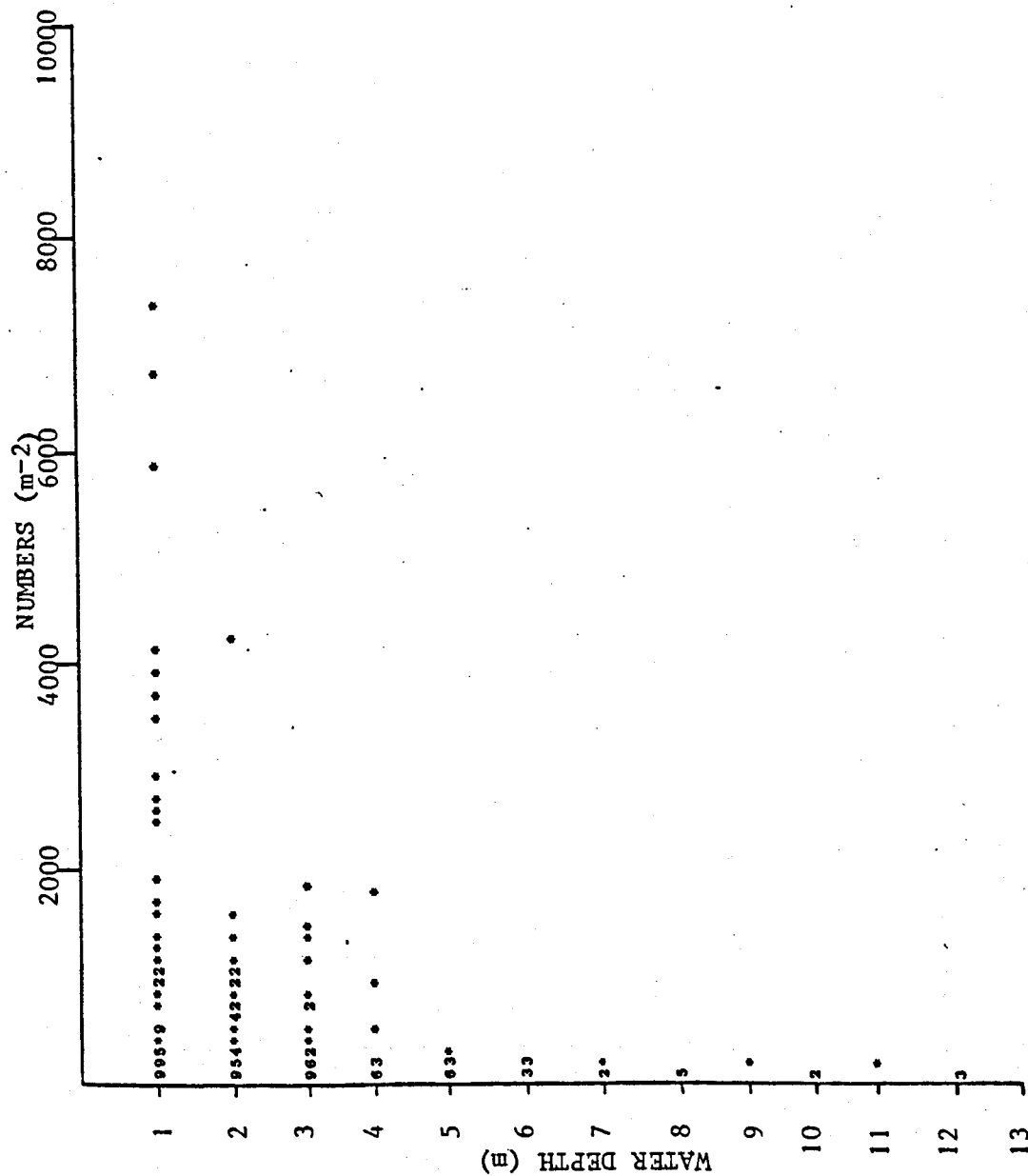


Fig. 50. Depth distribution of Psectrocladius larvae based on grab samples collected from the second north-arm and second south-arm transects throughout the study.

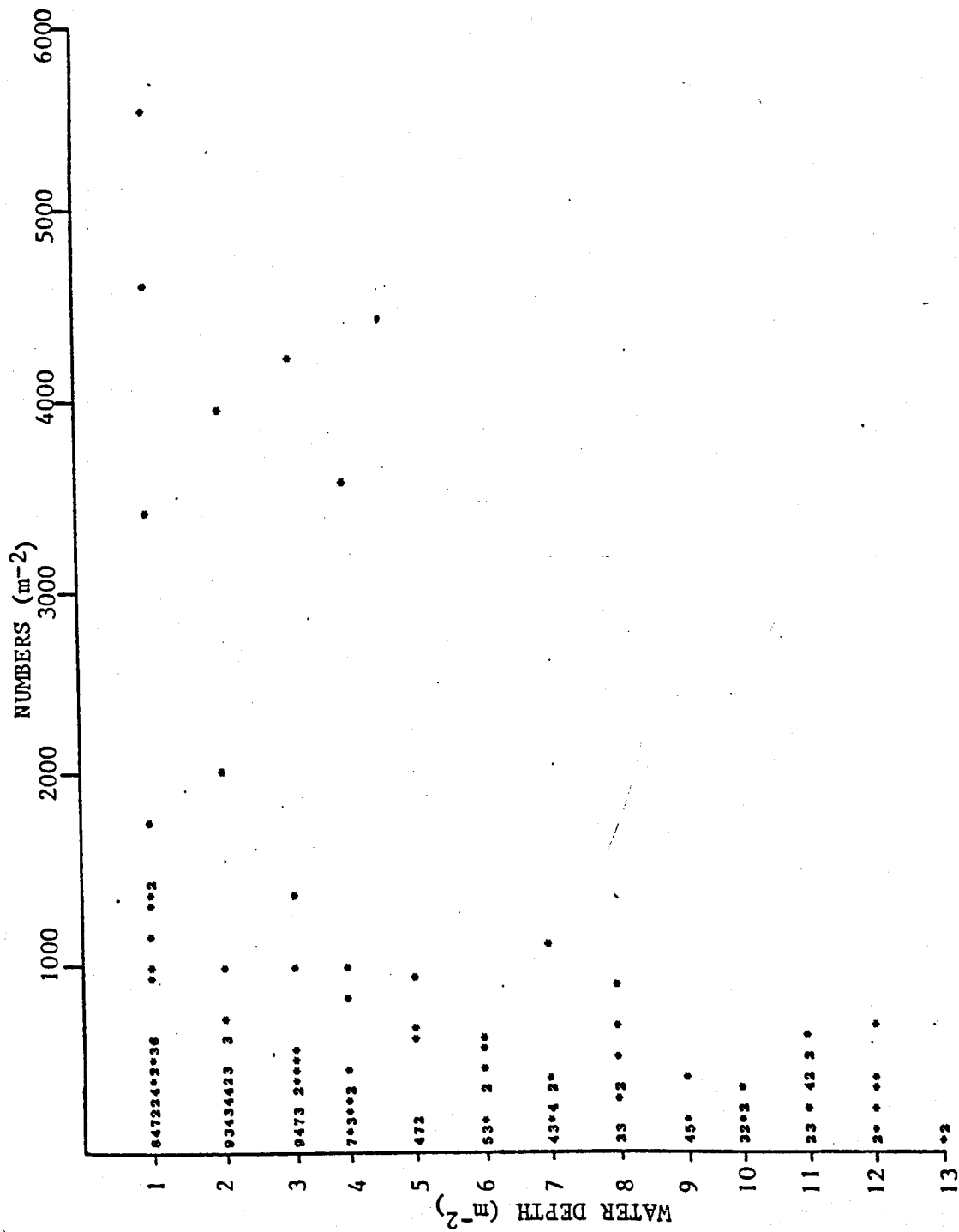


Fig. 51. Depth distribution of Chironomus larvae based on grab samples collected from the second north-arm and second south-arm transects throughout the study.

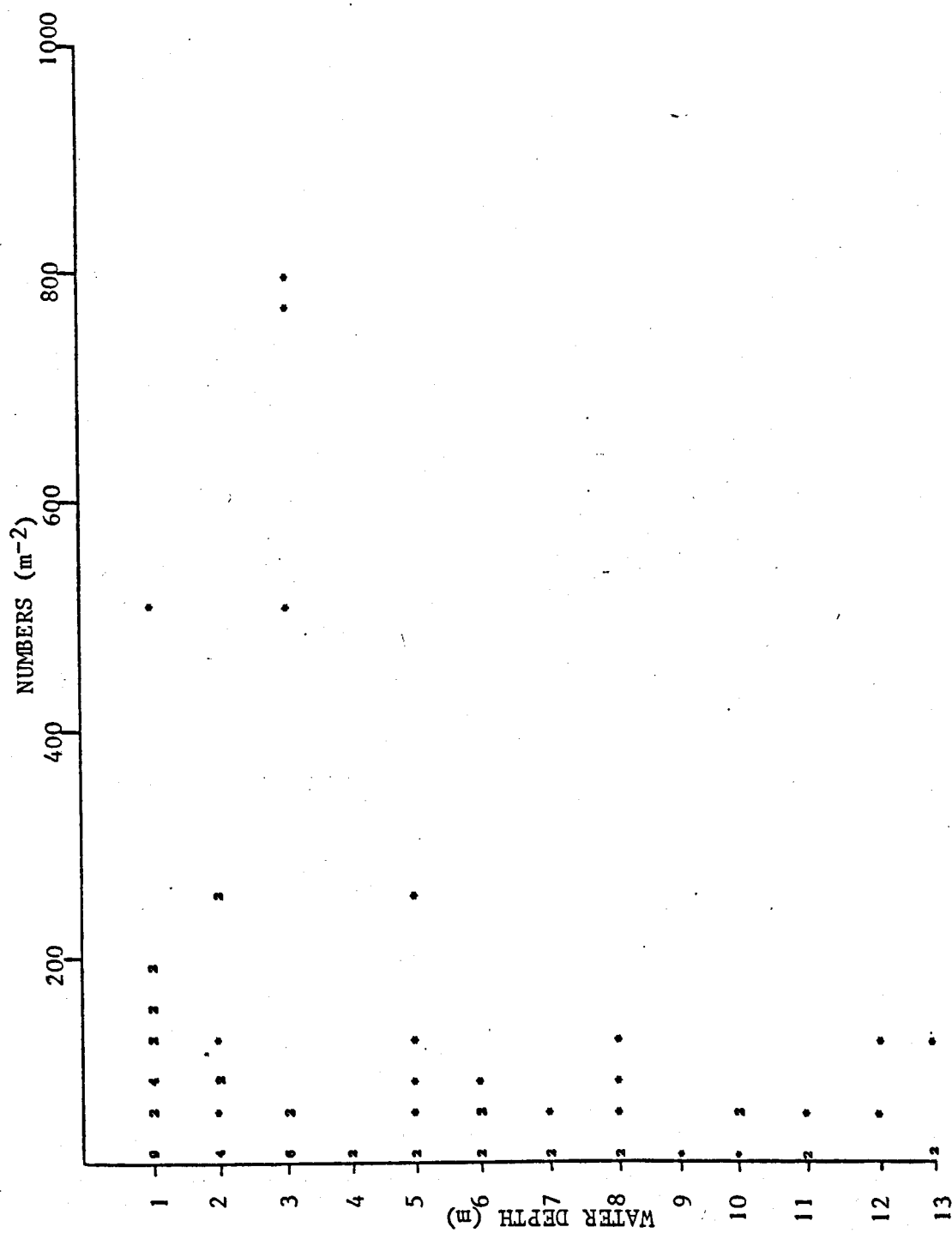


Fig. 52. Depth distribution of Cryptochironomus larvae based on grab samples collected from the second north-arm and second south-arm transects throughout the study.

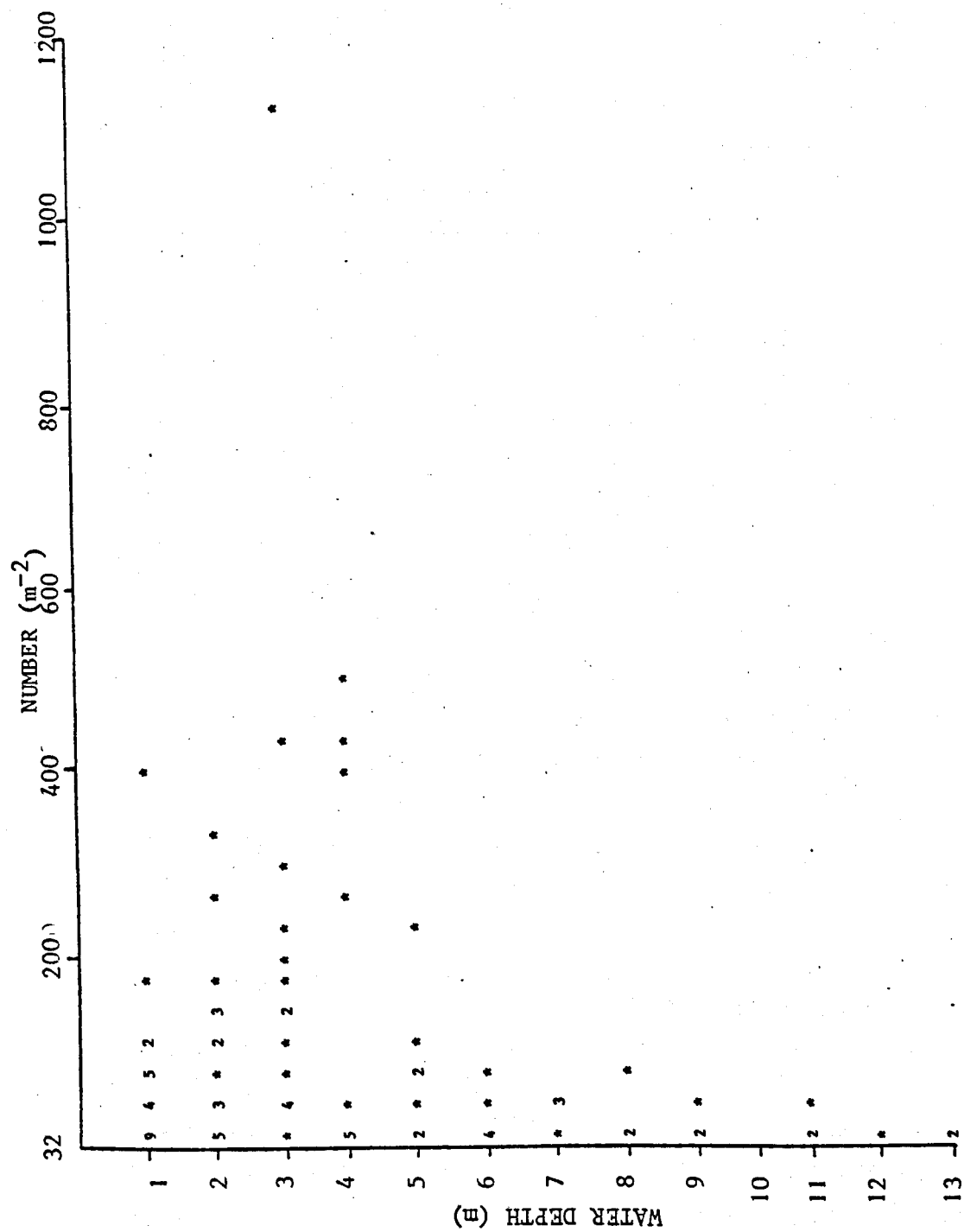


Fig. 53. Depth distribution of *Endochironomus* based on grab samples collected from the second north-arm and second south-arm transects throughout the study.

tower transect, but in low numbers. This species is known to be a typical inhabitant of algal mats in eutrophic lakes (Menche, 1939) and has been recorded as building tubes on the surfaces of leaves of aquatic plants (Walshe, 1951). The depth distribution was similar to that recorded by Mundie (1957) although the optimum depth he reported was 1-2m, slightly shallower than at Rutland Water. Laboratory observations of E. albipennis collected from Rutland Water confirmed that the larvae are able to build tubes on a mud substrate and could, therefore, occur at depths greater than the limit for plant growth.

Two species of Glyptotendipes were recorded in Rutland Water, G. pallens and G. paripes; the latter was more abundant. The highest population densities were recorded between 0-3m and some individuals were recorded down to 11m (Fig. 54). However, densities were too low to be certain of the depth distribution. The ecology of G. paripes was studied by Wundsch (1943) in the littoral zone of eutrophic lakes. Unlike other species of Glyptotendipes it was not found to be a leaf miner and the depth distribution was recorded as 2-3m. G. pallens has been recorded as a leaf miner in macrophytes (Walshe, 1951; Opalinskii, 1971) but Mackey (1976) states that it is not an obligate mining species as long flimsy tubes made by this species were recorded from the Acorus zones of the River Thames. The almost complete absence of macrophytes from Rutland Water suggests that the larvae were not leaf mining forms.

Microtendipes larvae, predominantly M. chloris, were recorded in approximately uniform densities down to 23m in the tower transect (Fig. 55). The highest densities were recorded at 3m. Lenz (1941) states that M. chloris occurs in both lotic and lentic habitats and builds sand tubes. In contrast to Rutland Water Mundie (1957) did not find this species in the profundal zone of Kempton Park Reservoir.

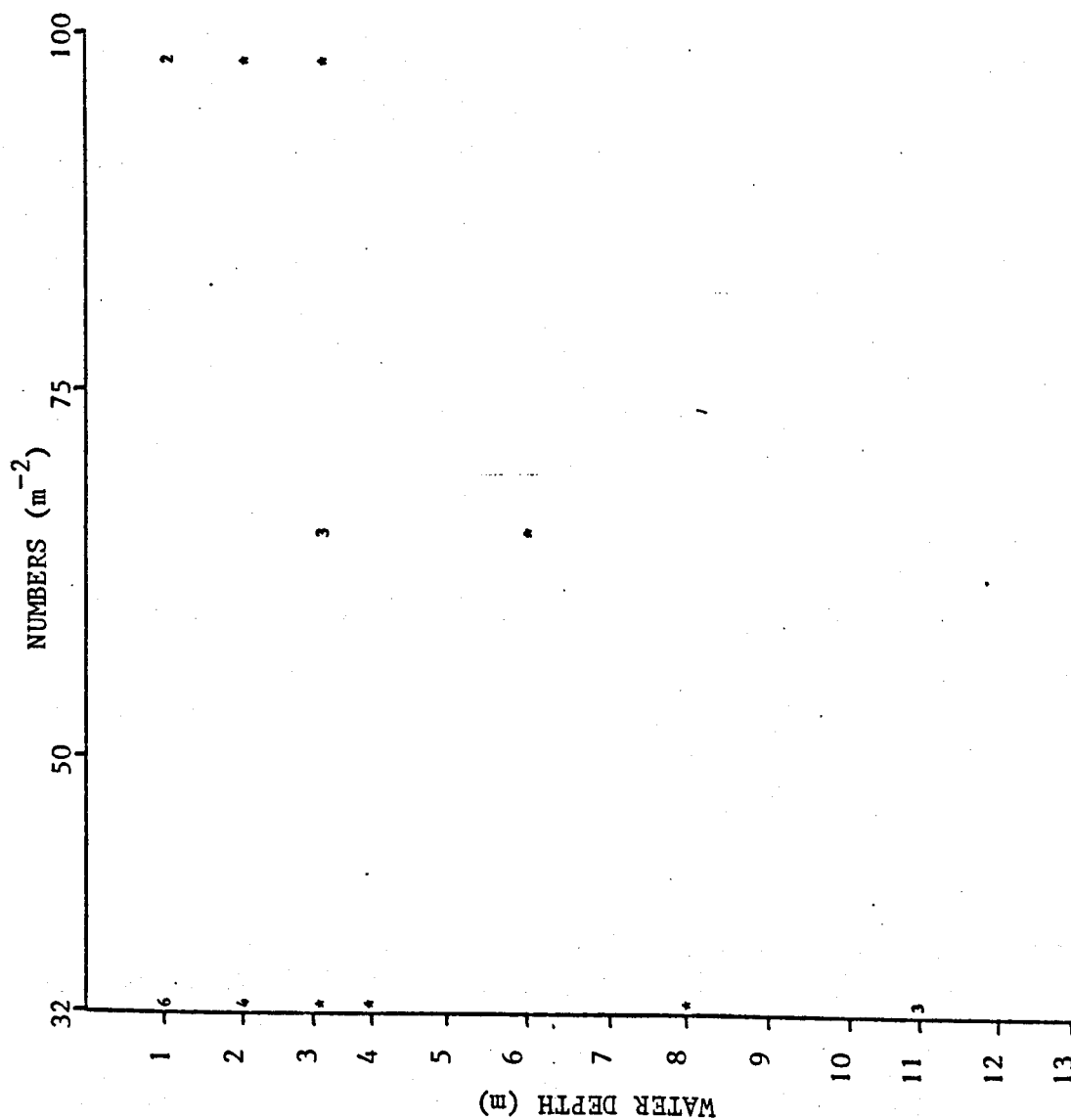


Fig. 54: Depth distribution of *Glyptotendipes* larvae based on grab samples collected from the second north-arm and second south-arm transects throughout the study.

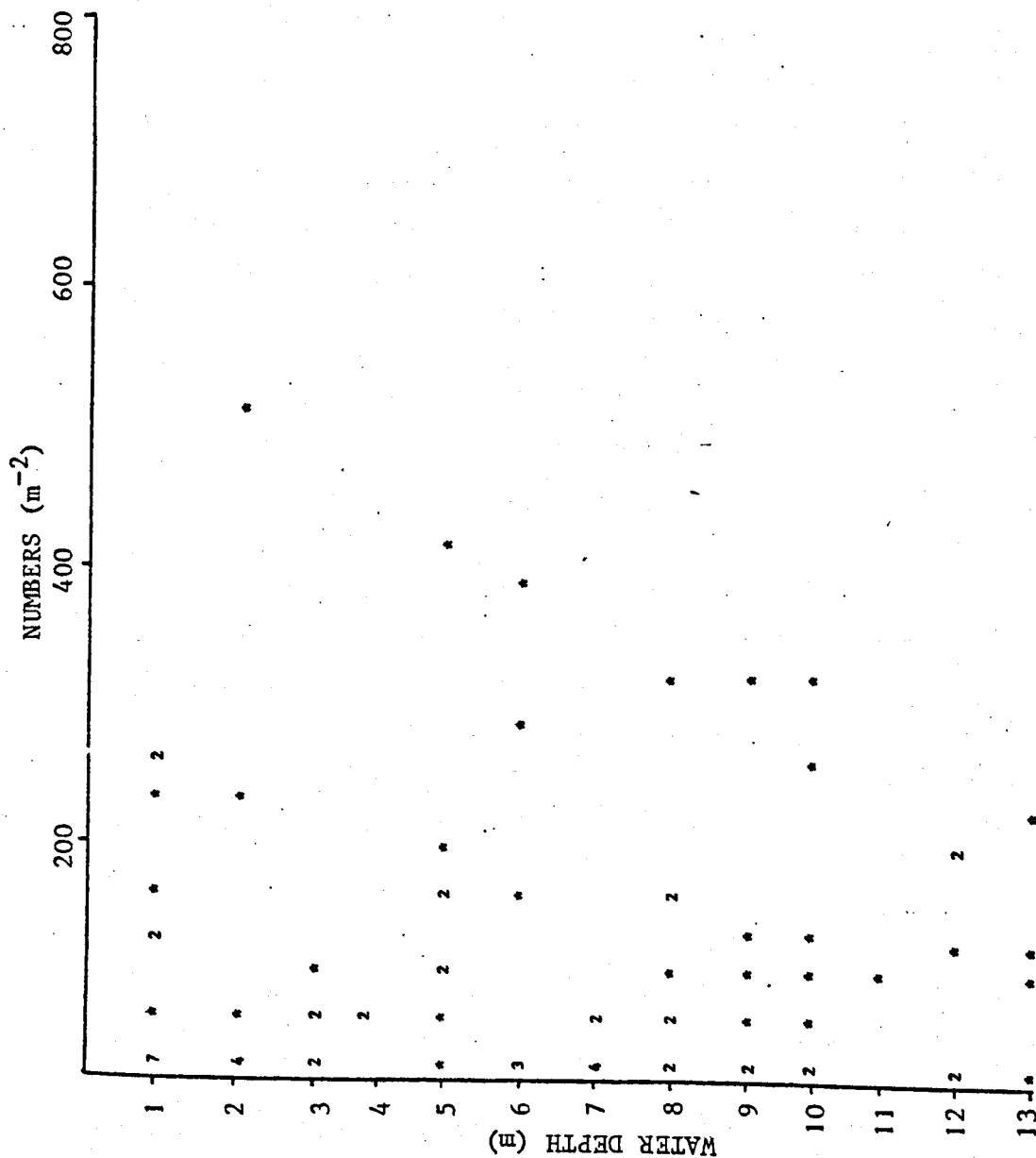


Fig. 55. Depth distribution of *Microtendipes* larvae based on grab samples collected from the second north-arm and second south-arm transects throughout the study.

Polypedilum nubeculosum showed a similar distribution to M. chloris, although the larvae occurred in larger numbers (Fig. 56). P. nubeculosum is a common species in eutrophic lakes and has a wide geographical distribution (Mundie, 1957). Sandberg (1969) found this species in the littoral zone of Lake Erken, but it is unlikely to have been restricted to this zone.

Six species of Tanytarsus and one species of Microsepectra have been recorded at Rutland Water but are treated together as Tanytarsini. The Tanytarsini as a whole are widely regarded to be characteristic species of oligotrophic lakes and favour well aerated water (Thienemann, 1925; Miyadi, 1933; Brundin, 1949). Results from Rutland Water and elsewhere (Mundie, 1957; Cantrell, 1975) indicate that some species of Tanytarsus can survive eutrophic conditions and even occur in the profundal zone of eutrophic waters. High population densities of Tanytarsini were recorded at Rutland Water down to 20m in the tower transect and the largest populations were recorded in shallow water (Fig. 57). T. lestagei, one of the more abundant species at Rutland Water, is an abundant species in oligotrophic lakes and may become abundant in shallow water in eutrophic lakes (Brundin, 1949). In the Großer Plöner See this species was found between 2-3m deep (Humphries, 1938). Another species from Rutland Water, T. holochlorus, was found in the littoral zone by Kruger (1945) and has also been found down to 20m by Humphries (1938).

Discussion

Comparison of the chironomid species composition and larval density of Rutland Water with other lakes and reservoirs is difficult due to the wide variety of sampling procedures, treatment of data, intensity of effort as well as changes and advances in taxonomy and identification keys. However, the general community composition is similar to other eutrophic reservoirs such as Eglwys Nunydd Reservoir (Potter and Learner, 1974) and Kempton Park East Reservoir (Mundie, 1954). Approximately 12 of the 34 species recorded by Potter and

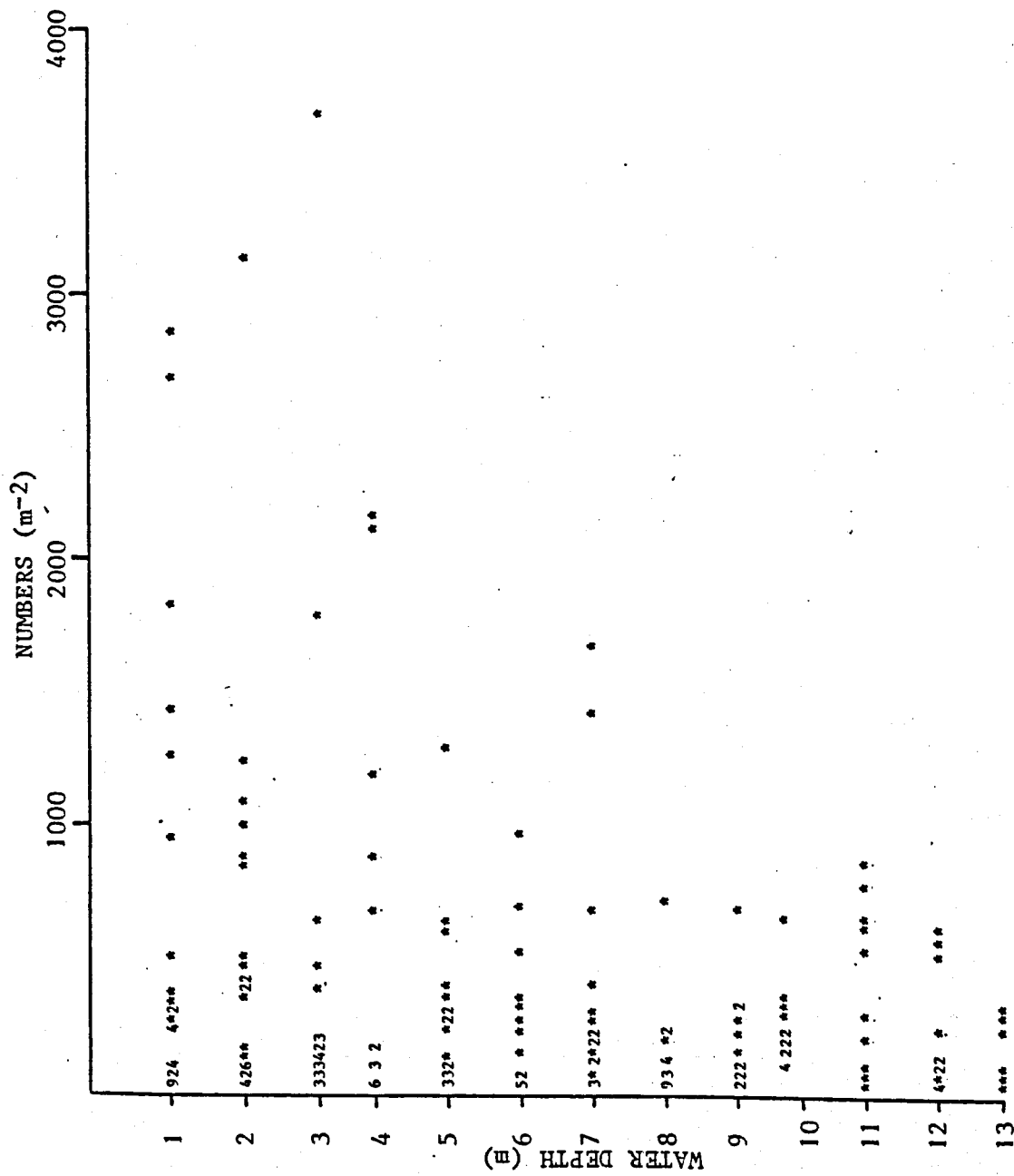


Fig. 56. Depth distribution of *Polypedilum* larvae based on grab samples collected from the second north-arm and second south-arm transects throughout the study.

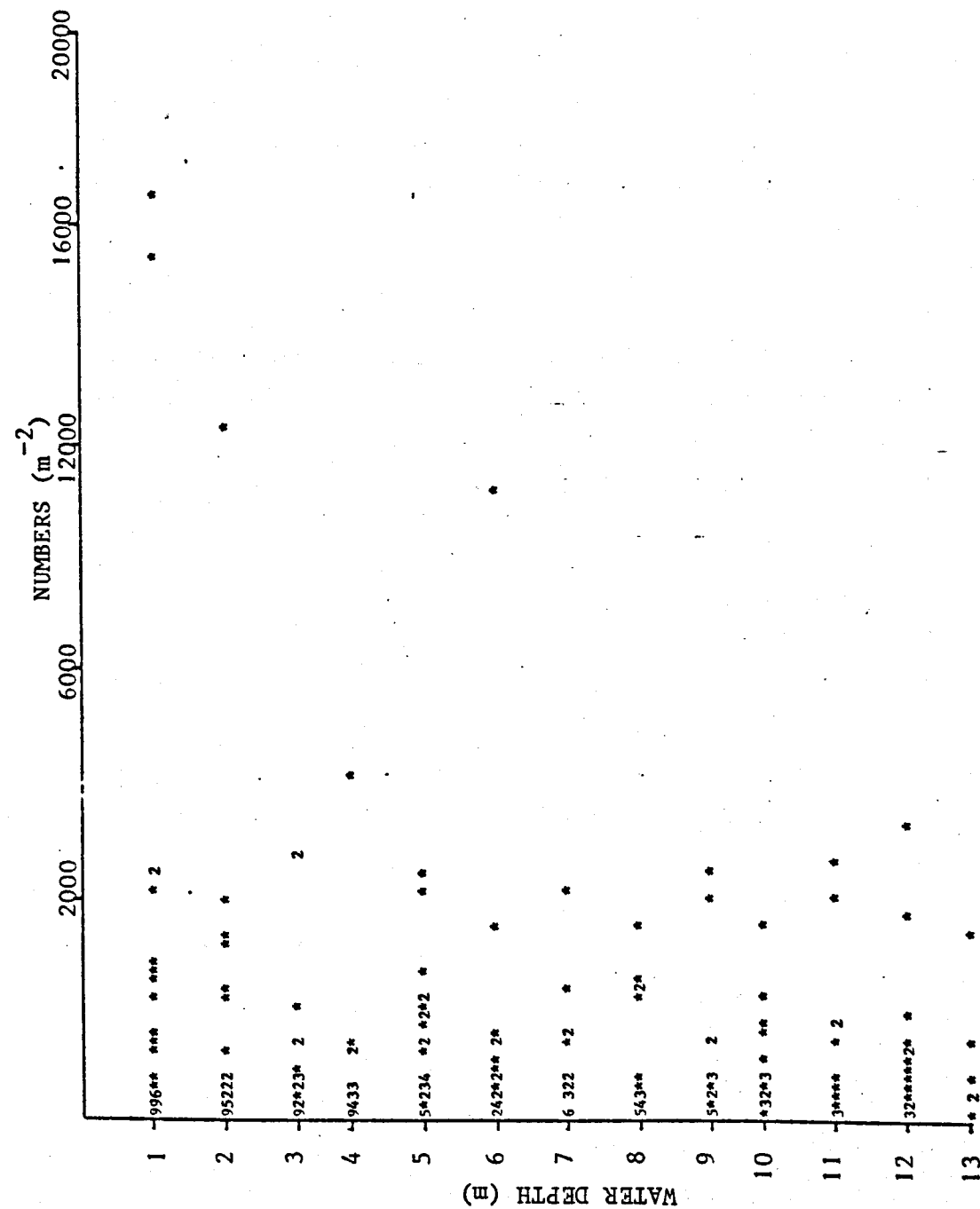


Fig. 57. Depth distribution of Tanytarsini based on grab samples collected from the second north-arm and second south-arm transects throughout the study.

Learner (1974) and 23 of the 58 species recorded by Mundie (1954) were recorded at Rutland Water. The number of species within different subfamilies at 3m deep for each of the reservoirs was similar except for the Orthocladiinae where a large number of species was recorded at Rutland Water (Table 35). The proportion of each of the groups also varied between the reservoirs. The Chironomini decreased in importance and the Tanytarsini increased in importance at Rutland Water compared with the other two reservoirs (Table 35). This may be due to the fact that Rutland Water is at an earlier stage of development and that the substrate does not favour the colonisation by Chironomini. The mean annual population density of chironomid larvae at Rutland Water, approximately $20,000\text{m}^{-2}$ (0-5m deep, sieve mesh size $500\mu\text{m}$) is lower than that recorded by Potter and Learner (1974), $30,000\text{m}^{-2}$ over the whole reservoir (mean depth 3.5m, sieve mesh size $150\mu\text{m}$) but similar to that recorded by Charles et al. (1974) at eutrophic Loch Leven, $24,000\text{m}^{-2}$ in 1971 and $14,000\text{m}^{-2}$ in 1972 (sandy littoral area, sieve mesh size $500\mu\text{m}$).

In contrast to these three eutrophic lakes, data from oligotrophic Lake Ankarvattnet, Sweden (Grimas, 1961) are also given in Table 35. Although a similar number of species is present, the Orthocladiinae account for over 55% of the total chironomid fauna. The Chironomini comprise a lower proportion of the total fauna and fewer species are present. Of the total of 56 species recorded in this lake only 5 were recorded in Rutland Water. Generally population densities of chironomid larvae are considerably lower in oligotrophic lakes and reservoirs. For example, in Lake Kultsjon, another oligotrophic Swedish lake, the population density recorded in the 0-5m depth zone was $3,000\text{m}^{-2}$.

As Rutland Water is at an early stage of development chironomid populations are in the process of successional changes and, therefore, comparisons with more mature lakes and reservoirs should be treated with caution. The successional changes in the chironomid fauna at Rutland Water are generally in good agreement with the four stages proposed by Morduchai-Boltovskoi (1961). The first stage is characterised by the occurrence of terrestrial invertebrates and the proliferation of

Table 35: Major subfamilies of Chironomidae in three eutrophic reservoirs, Eglwys Nunydd (Potter and Learner, 1974); Kempton Park East (Mundie, 1957); Rutland Water and one oligotrophic lake, Ankarrattnet (Grimas, 1961). Depths or depth zones from which data are taken are given in parenthesis.

	Eglwys Nunydd (3m)		Kempton Park East (3m)		Rutland Water (0-5m)		Ankarrattnet (2-4m)	
	No. Species	%	No. Species	%	No. Species	%	No. Species	%
Tanypodinae	4	12	4	13	5	21	5	9
Orthoclaadiinae	6	17	5	17	22	13	25	55
Chironomini	17	50	15	50	16	33	7	16
Tanytarsini	7	21	6	20	7	33	7	20
Total Number of Species (all depths)	34		58		50		56	

certain members of the river fauna. Few data are available for Rutland Water on the origins of the early colonising chironomid species. However, in the first samples collected by pond net from the reservoir in 1975, eight of the ten genera previously recorded in the River Gwash were found.

In the second stage of the classification proposed by Morduchai-Boltovskoi (op. cit.) there is a proliferation in a few dominant species, particularly Chironomus plumosus. At Rutland Water C. plumosus was recorded from the beginning of 1975 and gradually increased in numbers to a maximum population density of $5,500\text{m}^{-2}$ recorded in September 1977 in the second north-arm transect. At this time Chironomus larvae made up 58% of the total chironomid fauna in the reservoir. The larvae were generally confined to areas with some sediment and did not occur on newly inundated vegetation. Investigations by McLachlan and Cantrell (1976) showed that larval abundance of this species was positively correlated with sediment depth in the range 0-10mm. The development of a sediment layer is thus a prerequisite for invasion and colonisation by certain chironomid species.

Procladius, Chironomus and Polypedilum larvae were all present in large numbers in the reservoir in the second year after impoundment (1976). The proportion of Procladius in the benthos has remained approximately the same throughout the period whilst Chironomus has shown a decline in the third and fourth years and Polypedilum showed only a slight decline (Fig. 33). Procladius larvae are known to be free living and facultative predators (Kajak and Dusoge, 1970) and in adverse conditions they utilise other food items, mainly detritus (Barker and McLachlan, 1979). The larvae are also known to crawl rapidly on the substrate, $1.4 \pm 0.6\text{m day}^{-1}$ (McLachlan, 1975) but may also be found throughout the water column where they are distributed by water currents (Davies, 1973). It is probable that all these features of larval behaviour contributed to its success as an early coloniser in Rutland Water. Morduchai-Boltovskoi (1961) and Lellack (1966) have suggested that the increase in population density of C. plumosus larvae during the second stage of Morduchai-Boltovskoi's classification is associated with the decomposition of allochthonous

material resulting in low oxygen concentrations which these larvae can survive (Walshe, 1947, 1950). Several other factors may also contribute to the colonisation success of this species, for example increased powers of dispersal of large adults (Roff, 1977); abundance and wide distribution (Oliver, 1971); high biotic potential (Oliver, op. cit.) and extended emergence period as recorded at Rutland Water. Polypedilum has been recorded as an early coloniser of new reservoirs by several workers (Paterson and Fernando, 1970; Aggus, 1971). In Rutland Water maximum population densities of Polypedilum were recorded in the winter period 1976-77. In the following two winters these populations generally declined. The reason for this is unknown, but it may be related to a general decline in productivity of the reservoir, as nutrients released from the terrestrial vegetation are used up, or to some biotic change such as competition with other benthic species.

Endochironomus, Glyptotendipes and Microtendipes were all present in the reservoir in 1976 but declined in numbers in 1977. Endochironomus and Glyptotendipes have both been recorded as early colonisers of new reservoirs (Paterson and Fernando, 1970; Aggus, 1971) and Endochironomus has been recorded as one of the earliest colonisers on various substrates (Kalugina, 1959). The reason for the decline in relative abundance of these species in Rutland Water is not known. Aggus (1971) found that the decline in relative abundance of Glyptotendipes species in Beaver reservoir during the second and third years of filling was correlated with siltation.

The largest populations of Cricotopus and Psectrocladius larvae were recorded in summer 1976. This was a warm period (see Chapter 2) with a relatively stable water level, the populations built up in shallow water apparently thriving in the extensive beds of benthic algae. Their rapid decline in numbers at the end of 1976 was probably due to an increase in water levels as well as a seasonal decline. Orthocladiinae larvae appeared in subsequent years but in lower numbers.

The third stage of Morduchai-Boltovskoi (1961) is characterised by a decline in biomass of C. plumosus and their replacement by a number of chironomid species as well as other invertebrate groups such as oligochaetes and molluscs. The decline in the population density of C. plumosus larvae began in 1977 at Rutland Water, the third year after the start of filling. Kajak (1964) found that early instars of C. plumosus are poor competitors with other larvae and this may account for their decline. During 1977 and 1978 populations of Tanytarsus spp. increased. By the early part of 1979 this was the numerically dominant group of chironomids in the reservoir. Passivirta (1972) considers some members of the genus to be 'pioneer' species in new habitats. It is likely that conditions were suitable for Tanytarsus in 1975 and 1976 but competition with C. plumosus larvae, suggested by Cantrell and McLachlan (1977), may have prevented an increase in density of C. plumosus. A number of previously unrecorded species in Rutland Water were found towards the end of 1978 and early 1979, Ablabesmyia phatta, Camptochironomus tentans, Glyptotendipes pallens, Limnochironomus nervosus, Parachironomus vitiosus and several species of Tanytarsus.

There is no evidence that the fourth stage proposed by Morduchai-Boltovskoi (1961), the equilibrium stage, has been reached at Rutland Water.

Seasonal changes in the population densities of the eight most abundant chironomid taxa in Rutland Water were described for four different depth zones. From the larval data available, trends in emergence periods generally appear to follow those recorded by other workers. However, the sampling period employed here, approximately one month, is too long to determine the emergence periods of species with short generation times. Data from collections of pupal exuviae indicated that several species had long periods of emergence, although the main emergence may be over a short period. The composition of the pupal exuvial sample does, however, depend upon the length of time different exuvial types float, the effect of wind and wave action and their rate of decomposition. In the River Chew, Wilson and Bright

(1973) found exuviae had a half-life of approximately 2 weeks in the spring and 1 week in the autumn. It is also possible that the smaller and more delicate forms such as the Tanytarsini will be destroyed before the larger types such as the Chironomini. Given the sampling intervals usually employed at Rutland Water (2 to 4 weeks) it is likely that each sample is representative of the species that had emerged since the previous sample.

Annual variation in benthic invertebrate standing stocks have been recorded by several workers (for example Lundbeck, 1926; Eggleton, 1952; Jonasson, 1972; Charles et al., 1975). Many factors may cause these year to year variations, for example life history patterns, success of breeding, mortalities due to oxygen deficits. Climatic factors are thought to have played a major role in the development of Rutland Water. In 1976 low rainfall and high temperatures resulted in "drought" conditions. Filling of the reservoir stopped and benthic communities developed rapidly in the warm water. However, in the latter half of the year high rainfall enabled the filling programme to recommence and this altered benthic invertebrate populations. Orthoclaadiinae larvae, in particular, declined in abundance during the rise in water level. Large areas of newly flooded terrestrial vegetation were made available for colonisation by those species adapted to survive the changing conditions. The reservoir water level remained relatively stable from about May 1977 to the end of the study (Fig. 16).

Climatic differences between years may also affect the severity and duration of oxygen deficit as a result of thermal stratification or ice cover. Each year from 1975 to 1979 the reservoir began to show signs of stratification in May in the central basin area (Fig. 20). The extent of the thermocline and its duration in 1977 is unknown. In 1978, the main period of study, the thermocline was not persistent, possibly being disrupted by wind action. It is likely that in Rutland Water the extent of the thermocline will be restricted to the central basin area and will only be of short duration in the year. Migration of larvae out of the deeper water areas at the onset of stratification may

occur as described by Gerking (1962) and some changes in the growth rates and emergence periods of certain chironomid species may also occur (Bardach, 1955; Jonasson, 1965).

In January and February 1979 the temperature was below the decade mean (Fig. 3) and for a short period the reservoir was covered by ice. This results in a reduction in the oxygen content of the water and mortality of chironomid larvae may have occurred. This may partly account for the low population densities recorded at the beginning of 1979.

Considerable differences in chironomid population densities and species composition were found between different areas of the reservoir. Mathematical models were derived, using Taylor's power law to describe the spatial dispersion patterns of the numerically abundant chironomid taxa present. Utilising data from all six transects over the whole sampling period all taxa were found to be contagiously distributed (Fig. 42). Paterson and Fernando (1971) found that the dispersion patterns of two species of chironomid larvae were related to the population density. At low population densities they were contagiously distributed and at high population densities they were randomly distributed. At Rutland Water, as the larval population density changes monthly, several indices of dispersion were calculated monthly during 1978 for five abundant chironomid taxa. Populations tended to become more highly aggregated during the months of low population density (Tables 26 to 31). This supports the findings by Paterson and Fernando (1971); however, the aggregation may not simply be the result of low densities but a response to some environmental factor. The chironomid larval pattern within one substrate and at one depth in Rutland Water was found to be more randomly distributed than had been indicated by combined data from different parts of the reservoir. This contradicts the view of Paterson and Fernando (1971). However, in their investigation a low population was considered to be $1,000\text{m}^{-2}$ and in this investigation much lower population densities were recorded. A number of authors have recorded chironomid larvae as

being randomly distributed (for example Alley and Anderson, 1968; Ricker, 1952). In these and in the present study the effect of quadrat size was not investigated and as Elliott (1971) points out this can influence the detection of non-randomness. Elliott (op. cit.) also points out that a random distribution is a good hypothesis at low population densities as a small sampler ($< 0.05\text{m}^{-2}$) will not detect a contagious distribution if there are only a few individuals in each clump.

Spatial variation in the chironomid fauna at Rutland Water may be due to substrate differences that occur between sampling transects, for example extensive growths of filamentous algae were recorded in the second north-arm transect but not in the second south-arm transect. This is due to the more steeply shelving shoreline, the greater mean depth and the more exposed location of the second south-arm transect. As a result the second north-arm transect has a high population density of Orthocladiinae larvae whilst the second south-arm transect has a high population density of Tanytarsini larvae.

The morphometry of the reservoir basin and the input of pumped river water into the south-arm of the reservoir are also likely to produce spatial variations in the chironomid community. However, the analysis of the dominant chironomid taxa occurring at different transects indicated the dynamic nature of the community with the fauna changing in both numbers and species composition from month to month. On the basis of chironomid data alone no clear similarity between the two transects in the north-arm or between the two transects in the south-arm could be determined.

Investigation of the population changes of chironomid taxa within different depth zones revealed that larvae behave differently at different depths. Using data from the second south-arm transect and second north-arm transect depth distribution profiles for different chironomid taxa were calculated. Generally these agreed with the depth distributions given in published data. Brinkhurst and Walshe

(1967) demonstrated that the distribution of benthos with depth varies with time. Gerking (1962) believes that these changes are brought about by horizontal movements of larvae especially in response to oxygen deprivation. However, Dugdale (1955) suggests that different rates of development and hence different periods of emergence may account for the changes in depth distributions. Changes in the degree of predation at different depths may also account for changes in depth distributions of larvae. Insufficient data were available from Rutland Water to investigate seasonal changes in depth distributions of chironomid larvae.

CHAPTER 6

CHIRONOMIDS IN THE DIET OF TROUT

Introduction

An important aspect of managing Rutland Water as a trout fishery is a knowledge of the natural food supply available. As chironomid larvae form a major component of the benthos, their role in the diet of brown and rainbow trout was investigated. It is well known that chironomid larvae and, in particular, chironomid pupae may play an important part in the diet of trout in other lakes and reservoirs (Ball, 1961; Siddiqui, 1969; Hunt, 1970; Wilson et al., 1975; Pedley and Jones, 1978) but little work appears to have been carried out on new, lowland, eutrophic reservoirs. In February 1975 the reservoir began to fill and on 6th May 1977 the first fishing season commenced.

a) First fishing season May to October 1977

During the first fishing season at Rutland Water chironomids in the stomachs of 373 trout caught by fishermen were examined; 248 rainbow trout (mean length 342mm) and 125 brown trout (mean length 425mm). These fish were caught from most parts of the reservoir (Fig. 58) by boat and bank fishermen.

Data on chironomid larvae and pupae in trout stomachs in 1977 and 1978 are given in Appendix D and a preliminary published treatment of 1977 data (Brown, Oldham and Warlow, 1980) is given in Appendix E. Twelve genera of chironomid larvae were recorded in the stomachs. Micropsectra and Tanytarsus were not separated as genera and have been treated together as Tanytarsini. From the analysis of pupal exuviae the ratio of Micropsectra to Tanytarsus was approximately 1:12 in 1978 (Table 22). The composition of larvae in the diet of both trout species throughout the seven month sampling period is given in Table 36. Rainbow trout consumed a larger number of larvae (\bar{x} = 49) than brown trout (\bar{x} = 12). Only one of the two Tanypodinae genera was found

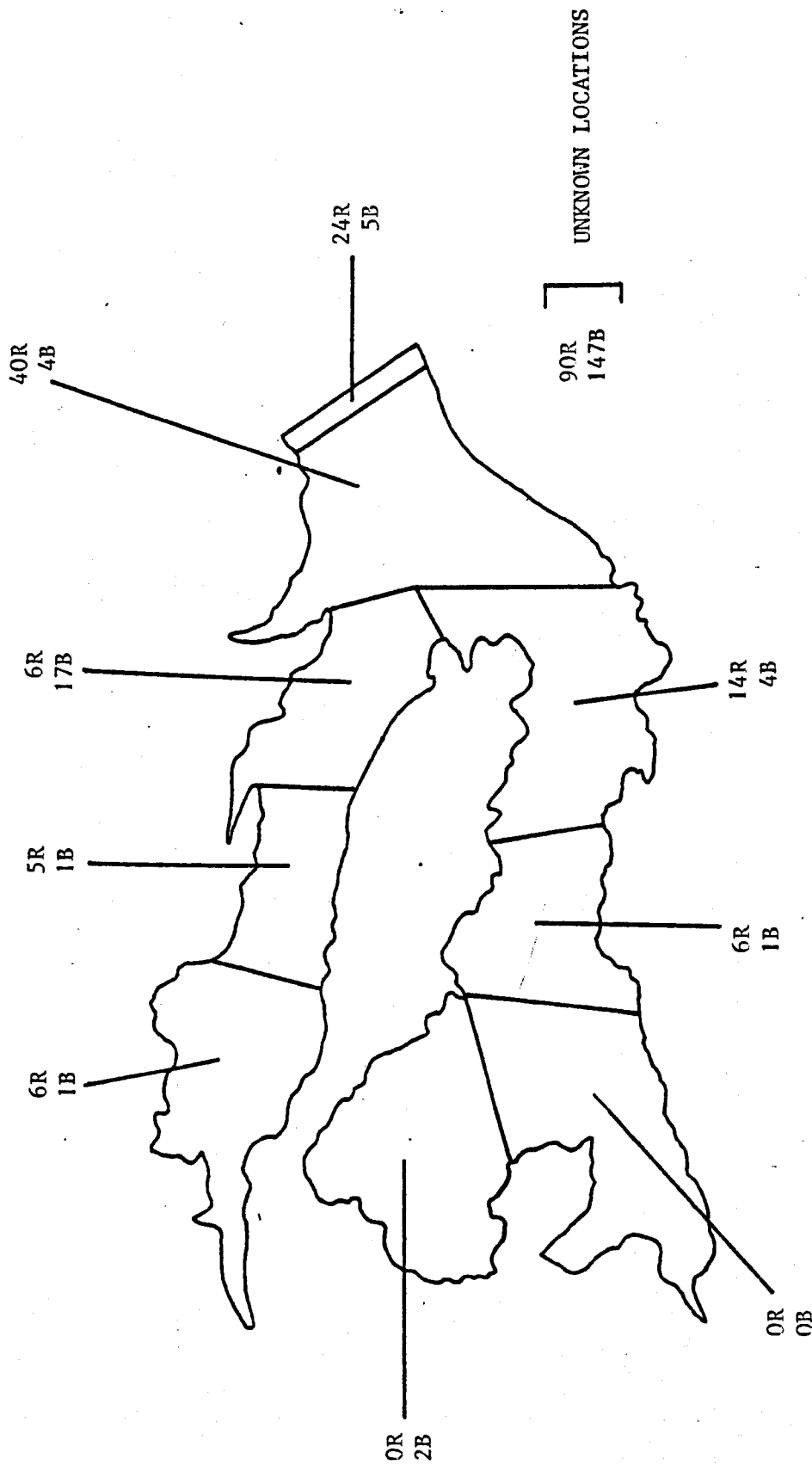


Fig. 58. Number of rainbow trout stomachs (R) and brown trout stomachs (B) collected from different areas of Putland Water in 1977.

Table 36: Chironomid larvae in the stomachs of rainbow and brown trout between April and October 1977

	Rainbow Trout (248 stomachs)			Brown Trout (125 stomachs)		
	Total No.	Mean No. per Stomach	% No. per Stomach	Total No.	Mean No. per Stomach	% No. per Stomach
Procladius	476	1.9	4.0	419	3.4	28.6
Ablabesmyia	6	< 0.1	< 0.1	6	< 0.1	0.4
Cricotopus	525	2.1	4.4	6	< 0.1	0.4
Orthocladius	12	< 0.1	0.1	1	< 0.1	< 0.1
Psectrocladius	2,469	10.0	20.5	182	1.5	12.4
Chironomus	109	0.4	0.9	223	1.8	15.2
Cryptochironomus	288	1.2	2.4	200	1.6	13.7
Endochironomus	7,952	32.1	66.0	367	2.9	25.1
Glyptotendipes	95	0.4	0.8	10	< 0.1	0.7
Polypedilum	73	0.3	0.6	39	0.3	2.7
Tanytarsini	43	0.2	0.4	12	0.1	0.8
Totals	12,041	48.6	100	1,465	11.7	100

in stomachs in large numbers. Cricotopus and Psectrocladius larvae were consumed in comparatively large numbers by rainbow trout. Larvae of these two genera are abundant in water less than 4m deep (Figs. 48 and 50). Endochironomus albipennis was the predominant Chironomini species consumed. This species was not found in large numbers in grab samples collected in 1977; the maximum population density (180 m^{-2}) occurred in August in the 0-5m depth zone (Fig. 38). The optimum depth recorded for this species was 4m (Fig. 53) although occasional specimens were found down to 23m. A comparison of the larvae found in trout stomachs (Table 36) with those found in the benthos throughout the sampling period (Table 19) reveals a number of genera that were not recorded in trout stomachs. These occurred at low population densities in the benthos and may not have been present in the reservoir during the trout stomach sampling period.

In order to gain an indication of the proportion of the organisms in the diet relative to the proportion in the benthos an index of selective feeding or electivity was calculated using the formula by Ivlev (1961):

$$E = \frac{(r_i - p_i)}{(r_i + p_i)}$$

where E = electivity index, r_i = proportion of the organisms present in the benthos, p_i = proportion of the organisms present in the diet. Positive electivity or selection for an organism is expressed by values from +1 to 0 and negative electivity by values from 0 to -1. Strong positive electivity for Endochironomus larvae was shown by rainbow trout (Table 37). Brown trout showed strong positive electivity for Cryptochironomus, Endochironomus and Glyptotendipes larvae. Electivity indices cannot be calculated for pupae as estimates of their abundance throughout the water column is not possible.

The composition of the pupal diet of trout is shown in Table 38. The mean number of pupae per fish was 45 compared to

Table 37: Electivity index for rainbow and brown trout relating the occurrence of chironomid larvae in the benthos and in fish stomachs.

	% No. in Benthos	Rainbow Trout		Brown Trout	
		% No/fish stomach	Electivity	% No/fish stomach	Electivity
Procladius	18.9	3.4	-0.69	29.0	+0.21
Ablabesmyia	0.5	<0.1	-0.89	0.4	-0.10
Cricotopus	5.5	3.3	-0.25	0.1	-0.95
Orthocladius	1.7	<0.1	-0.92	<0.1	-0.92
Psectrocladius	9.6	22.0	+0.39	12.5	+0.13
Chironomus	24.2	0.9	-0.93	15.3	-0.22
Cryptochironomus	2.1	2.4	+0.07	13.2	+0.73
Endochironomus	2.4	67.0	+0.93	25.2	+0.83
Glyptotendipes	0.2	<0.1	-0.67	0.7	+0.55
Polypedilum	7.1	0.5	-0.86	2.7	-0.45
Tanytarsini	27.4	0.4	-0.97	0.8	-0.94

Table 38: Chironomid pupae in the stomachs of rainbow and brown trout between April and October 1977

	Rainbow trout (229 stomachs)			Brown trout (104 stomachs)		
	Total No.	Mean No. per Stomach	% No. per Stomach	Total No.	Mean No. per Stomach	% No. per Stomach
Procladius	1,943	8.5	20.5	481	4.6	8.6
Ablabesmyia	76	0.3	0.8	2	<0.1	<0.1
Cricotopus	242	1.1	2.6	19	0.2	0.3
Orthocladius	211	0.9	2.2	631	6.1	11.3
Psectrocladius	1,954	8.5	20.6	165	1.6	3.0
Chironomus	1,568	6.9	16.6	2,638	25.4	47.1
Cryptochironomus	11	<0.1	0.1	96	0.9	1.7
Endochironomus	999	4.4	10.6	378	3.6	6.8
Glyptotendipes	2	0.1	<0.1	1	<0.1	<0.1
Microtendipes				2	<0.1	<0.1
Polypedilum	188	0.8	2.0	11	0.1	0.2
Tanytarsini	2,278	10.0	24.1	1,178	11.3	21.0
Totals	9,472	41.4	100	5,602	53.9	100

36 larvae per fish, and brown trout in particular consumed pupae ($\bar{x} = 54$) more heavily than larvae ($\bar{x} = 12$). Procladius, Endochironomus and Tanytarsini pupae were prominent in the diets of both species. Rainbow trout preyed more heavily than brown trout on Psectrocladius pupae and brown trout preyed more heavily than rainbow trout on Chironomus and Orthocladius pupae.

A oneway analysis of variance was used to test for significant differences in the larval and pupal diets of brown and rainbow trout. The null hypothesis is that both samples, i.e. diets, come from the same population and will, therefore, have the same variances. Significant differences at the 1% level occurred for three larval genera and five pupal genera (Table 39). Psectrocladius and Chironomus pupae showed the most significant differences. This indicates that rainbow trout feed extensively on Psectrocladius pupae, the larvae of which live in shallow water (Fig. 50) whilst brown trout feed extensively on Chironomus pupae whose larvae occur throughout the reservoir.

Seasonal changes for the five most abundant chironomid genera occurring in trout stomachs are shown in Figure 59. Although Procladius, Chironomus and Tanytarsini had the highest larval population densities in the benthos, few larvae were found in trout stomachs. The number of Psectrocladius larvae in trout stomachs showed little fluctuation from July to October 1977 whilst the number of Endochironomus larvae in stomachs showed a sharp increase in September 1977 ($\bar{x} = 90$ per stomach). Pupae of all five genera showed monthly fluctuations in mean number per stomach but the highest numbers were recorded in August and September (Fig. 59). Few pupae of any of the five genera were consumed in April, May or October 1977.

Three different methods of expressing the results of the stomach analysis have been employed to assess the importance of chironomids in the diet in relation to other organisms.

Table 39: Analysis of variance comparing the numbers of larvae and pupae in rainbow and brown trout stomachs ($p < 0.01$ is considered to indicate significant differences).

	Larvae		Pupae	
	F Value	Significance (p)	F Value	Significance (p)
Procladius	0.631	0.4274	2.466	0.1173
Ablabesmyia	0.401	0.5269		
Cricotopus	8.946	0.0030	7.581	0.0062
Orthocladius	2.244	0.1350	7.132	0.0079
Psectrocladius	8.114	0.0046	15.832	0.0001
Chironomus	4.103	0.0435	12.621	0.0004
Cryptochironomus	0.321	0.5711	2.682	0.1024
Endochironomus	9.665	0.0020	0.238	0.6263
Glyptotendipes	1.276	0.2594	0.006	0.9373
Microtendipes			14.463	0.0354
Polypedilum	0.007	0.9336	6.789	0.0096
Tanytarsini	0.374	0.5415	0.107	0.7434

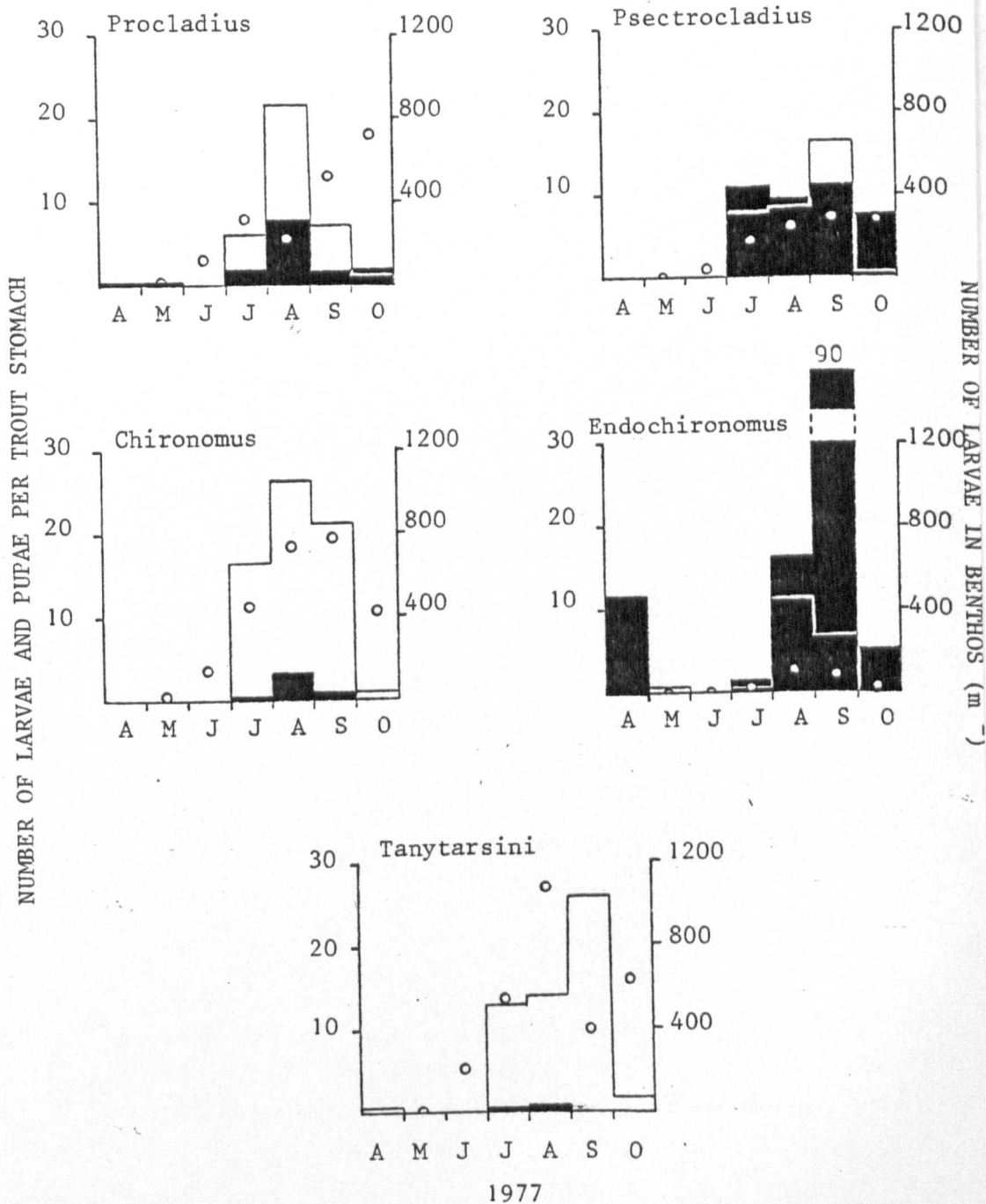


Fig. 59. Monthly changes in the mean number of larvae and pupae in trout stomachs and benthos in 1977. Black - larvae in stomachs; white - pupae in stomachs; o - larvae in benthos. No stomach samples in June.

$$\text{Percentage occurrence} = \frac{\text{No. stomachs containing food item } x}{\text{Total No. stomachs containing some food}} \times 100$$

$$\text{Percentage number} = \frac{\text{No. of food item } x \text{ in all stomachs}}{\text{Total No. of food items in all stomachs}} \times 100$$

$$\text{Percentage dry weight} = \frac{\text{Total dry wt. of food item } x \text{ in stomachs}}{\text{Total dry wt. of all stomach contents}} \times 100$$

The percentage occurrence indicates what proportion of the total trout sampled were feeding on that particular food item at that time. This gives no indication as to the actual numbers consumed, nor does it indicate the importance of a few large food items to the total diet. Percentage number and percentage dry weight have been calculated for this purpose.

A high proportion of the trout stomachs sampled contained chironomid larvae and pupae, particularly from July to October 1977 (Fig. 60). Larvae occurred more frequently than pupae in stomachs only in April and October. The percentage number of larvae and pupae in stomachs follows a similar trend to occurrence with the highest values occurring in the summer and autumn. The percentage number of larvae in stomachs is high in September due to the large numbers of Endochironomus larvae found. Chironomid larvae and pupae contributed 17% by dry weight to the diet over the whole sampling period, with pupae reaching a maximum of 38% in July 1978 (Fig. 60). The remaining composition of the stomach contents consisted of vegetation (29%), earthworms (22%), fish (11%), Lymnaea peregra (7%), Gammarus pulex (4%), Daphnia (2%) and others (8%) (Warlow, pers. comm.). Few aerial insects were found in stomachs during the sampling period.

- b) Second fishing season, April to October 1978 and comparison with the 1977 season

Prior to the 1978 fishing season a sample of 19 rainbow trout and 2 brown trout was obtained by beach seine netting. None

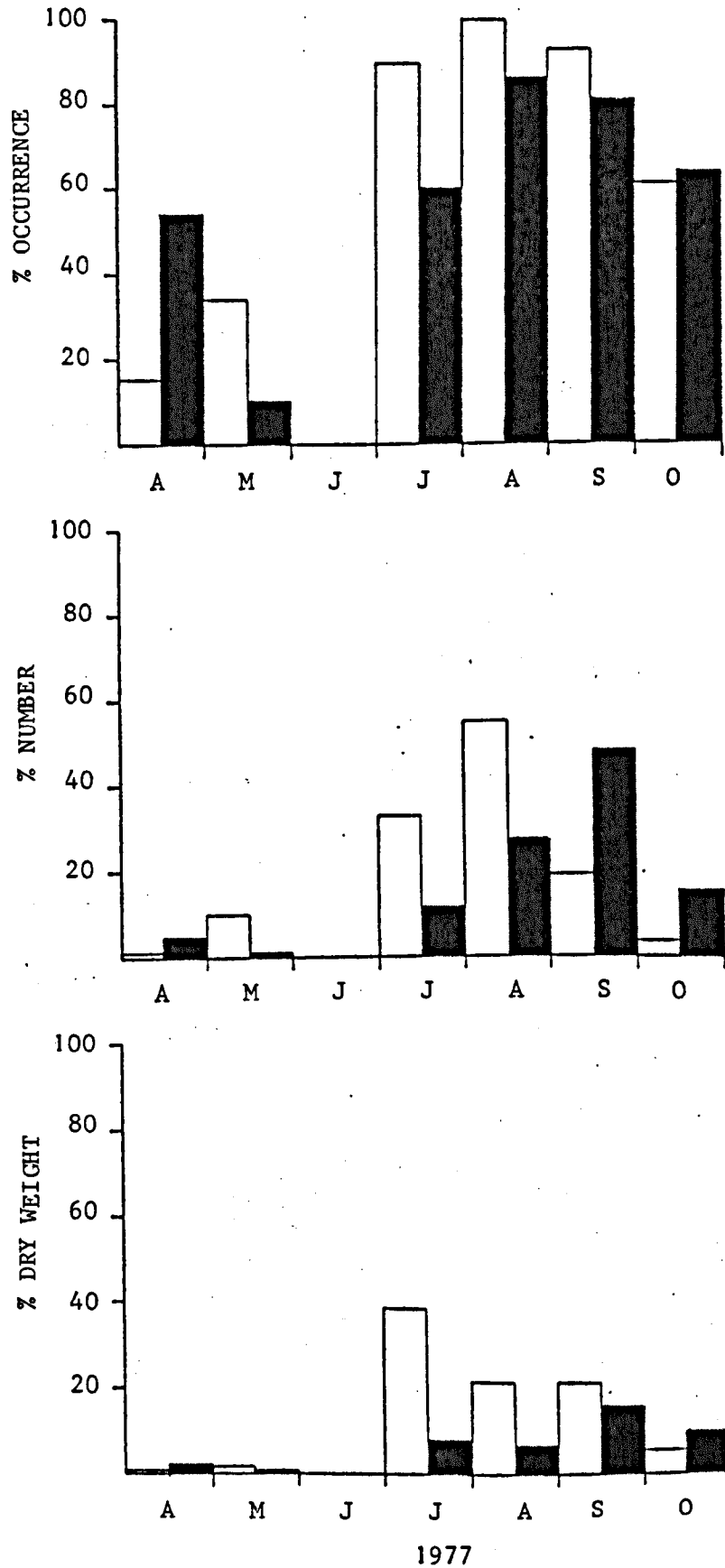


Fig. 60. Percentage occurrence, number and dry weight of chironomid larvae and pupae found in trout stomachs from April to October 1977. Black - larvae; white - pupae. No sample in June.

of the stomachs contained chironomid pupae and only 8 contained chironomid larvae. Psectrocladius and Chironomus larvae were most abundant and Microtendipes and Polypedilum larvae were also found. No data are available for chironomids in trout stomachs obtained prior to the opening season in 1977.

482 trout stomachs were collected between 4th April and 21st October 1978 from bank and boat fishermen. The rainbow trout had a mean length 344 ± 2 mm and mean weight 567 ± 12 g, brown trout had a mean length 362 ± 6 mm and mean weight 665 ± 33 g. Chironomids from 288 of these trout stomachs were obtained for analysis, 240 rainbow trout and 48 brown trout. The rainbow trout were similar in mean size to those obtained in 1977 but the brown trout were smaller.

Rainbow trout stomachs contained 12 genera of chironomid larvae whilst brown trout only contained 10; Ablabesmyia and Microtendipes were not recorded (Table 40). Psectrocladius larvae were consumed in the largest numbers by both species of trout, and the mean number of Psectrocladius larvae per stomach for both trout species was higher than in 1977. Rainbow trout consumed a slightly lower number of larvae per fish in 1978 ($\bar{x} = 36.3$) than in 1977 ($\bar{x} = 48.6$) whilst brown trout consumed a higher number in 1978 ($\bar{x} = 37.5$) than in 1977 ($\bar{x} = 11.7$).

Psectrocladius, Chironomus, Polypedilum and Tanytarsus accounted for 81% of the pupae consumed by rainbow trout and Chironomus, Microtendipes and Tanytarsus accounted for 63% of the pupae consumed by brown trout (Table 41). Rainbow trout consumed a larger number of pupae per fish in 1978 ($\bar{x} = 84$) than in 1977 ($\bar{x} = 41$) whilst brown trout consumed a lower number in 1978 ($\bar{x} = 22$) than in 1977 ($\bar{x} = 54$).

Seasonal changes in the number of larvae and pupae of the five most abundant taxa occurring in stomachs are shown in Figure 61. As in 1977, Procladius, Chironomus and Tanytarsini larvae all occur in relatively large numbers in the benthos whilst few larvae are found in stomachs (Fig. 61). Psectrocladius larvae were found in stomachs in large numbers in April, June and July 1978 compared

Table 40: Composition of chironomid larvae in the diet of rainbow and brown trout between April and October 1978

	Rainbow Trout (240 stomachs)			Brown Trout (48 stomachs)		
	Total No.	Mean No. per Stomach	% No. per Stomach	Total No.	Mean No. per Stomach	% No. per Stomach
Procladius	648	2.7	7.4	46	1.0	2.6
Ablabesmyia	8	<0.1	<0.1	0	0	0
Cricotopus	1,406	5.9	16.2	5	0.1	0.3
Orthocladius	569	2.4	6.5	2	<0.1	0.1
Psectrocladius	3,796	15.8	43.6	1,612	33.6	89.6
Chironomus	179	0.7	2.1	4	<0.1	0.2
Endochironomus	1,133	4.7	13.0	112	2.3	6.2
Glyptotendipes	358	1.5	4.1	6	0.1	0.3
Microtendipes	47	0.2	0.5	0	0	0
Parachironomus	19	<0.1	0.2	3	<0.1	0.2
Polypedilum	485	2.0	5.6	6	0.1	0.3
Tanytarsini	55	0.2	0.6	4	<0.1	0.2
Totals	8,703	36.3	100	1,800	37.5	100

Table 41: Composition of chironomid pupae in the diet of rainbow and brown trout between April and October 1978

	Rainbow Trout (240 stomachs)			Brown Trout (48 stomachs)		
	Total No.	Mean No. per stomach	% No. per stomach	Total No.	Mean No. per stomach	% No. per stomach
Procladius	1,140	4.8	5.6	5	0.1	0.5
Ablabesmyia	30	0.1	0.2	0	0	0
Cricotopus	416	1.7	2.1	0	0	0
Orthocladius	501	2.1	2.5	54	1.1	5.2
Psectrocladius	4,436	18.5	22.0	108	2.3	10.4
Chironomus	3,515	14.6	17.4	268	5.6	25.9
Cryptochironomus	8	<0.1	<0.1	1	<0.1	<0.1
Endochironomus	22	<0.1	0.1	20	0.4	1.9
Glyptotendipes	25	0.1	0.1	40	0.8	3.9
Microtendipes	1,898	7.9	9.4	172	5.6	16.6
Parachironomus	85	0.4	0.4	1	<0.1	<0.1
Polypedilum	4,468	18.6	22.1	148	3.1	14.3
Tanytarsus	3,623	15.1	19.9	209	4.4	20.2
Micropsectra	38	0.2	0.2	10	0.2	1.0
Totals	20,205	84.2	100	1,036	21.6	100

MEAN NUMBER OF LARVAE AND PUPAE PER TROUT STOMACH

MEAN NUMBER OF LARVAE IN BENTHOS (m^{-2})

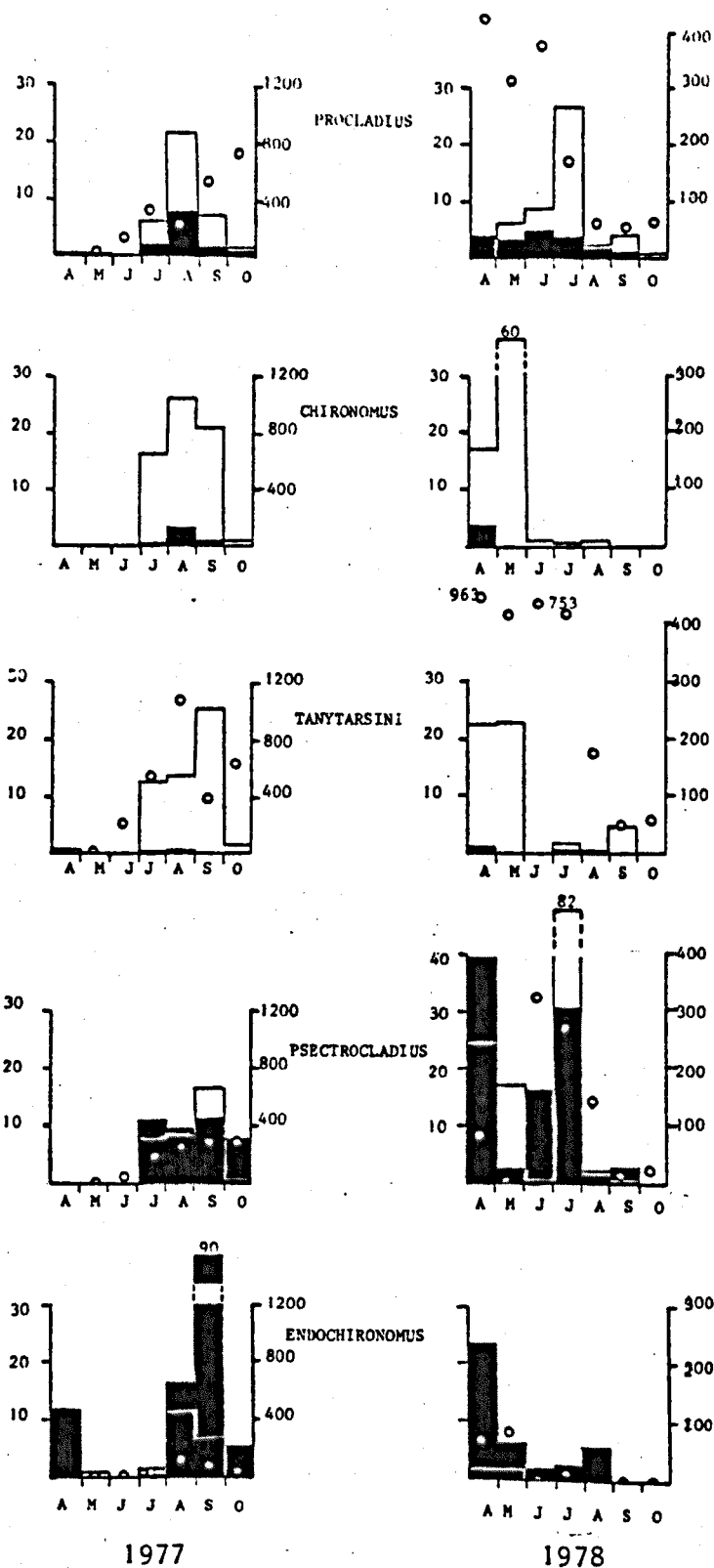


Fig. 61. Monthly changes in the mean number of larvae and pupae in trout stomachs and benthos in 1978. Data from 1977 shown for comparison. Black - larvae in stomachs; white - pupae in stomachs; o - larvae in benthos.

to July, August, September and October 1977. The largest number of Psectrocladius pupae was recorded in July 1978 (Fig. 61). In September 1977, 90 Endochironomus larvae per trout stomach was recorded, the highest value for that year; however, in September 1978 no Endochironomus larvae were found in trout stomachs. In none of the five taxa shown in Figure 61 did the seasonal maxima in 1978 for larvae or pupae, occur in the same month as in 1977.

Percentage occurrence, number and dry weight for larvae and pupae in trout stomachs for each month was calculated as described previously. More than 60% of the stomachs sampled in April, May and June 1978 contained chironomid larvae and pupae (Fig. 62). From July 1978 the number of stomachs containing larvae and pupae declined steadily to less than 20% in October. The highest percentage number of pupae in trout stomachs occurred in May 1978 (Fig. 62) whilst in 1977 the highest number occurred in August. The maximum percentage number of larvae consumed in 1977 occurred in September whilst in 1978 the maximum occurred in July and the minimum in September (Fig. 62). Chironomid pupae contributed 38% by dry weight to the total diet throughout the whole period in 1978, considerably higher than the 11% recorded in 1977. Larvae contributed only 4% by dry weight to the diet in 1978. The percentage dry weight that other food items contributed to the total diet throughout 1978 were: Gammarus pulex (13%), Lymnaea peregra (20%), vegetation (7%) and others (18%).

c) Discussion

Chironomid larvae appear to be eaten according to their accessibility to trout and not necessarily according to their numerical abundance in the benthos. Free-living species such as Procladius and the temporary tube dwellers, the Orthocladiinae, were consumed in large numbers as larvae, whilst the tubiculous forms, such as Chironomus and the Tanytarsini species, were consumed in comparatively small numbers. This agrees with the

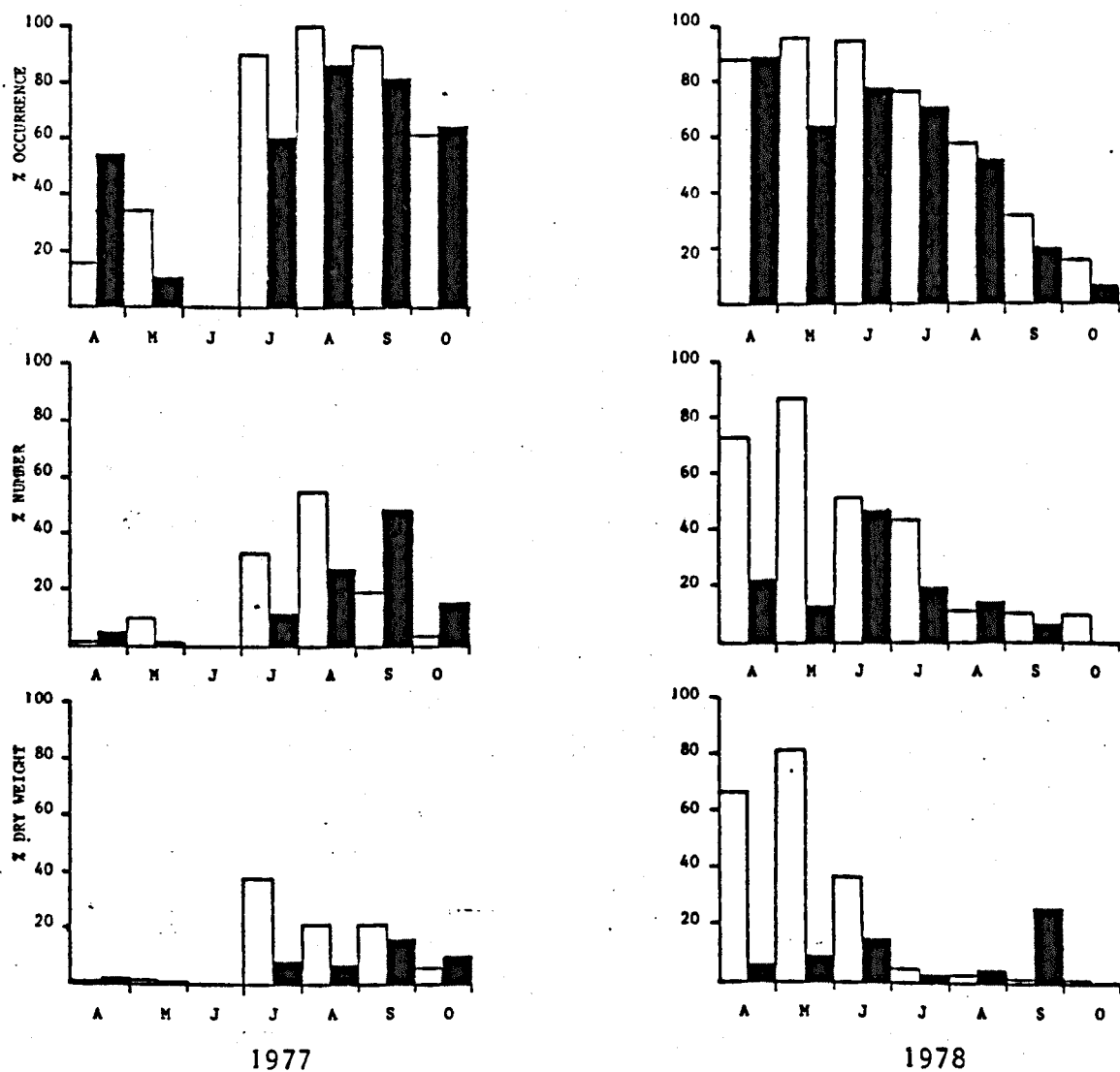


Fig. 62. Percentage occurrence, number and dry weight of chironomid larvae and pupae in trout stomachs from April to October 1978. Data from 1977 shown for comparison.

view put forward by Hunt (1970) that size, habits and mobility of the food organisms are more important than numbers in determining their presence in trout diet.

In 1977 Endochironomus albipennis was the exception to the low numbers of tubiculous Chironominae consumed at Rutland Water. Larvae occurred in large numbers in stomachs although the species was found to have relatively low population densities in the benthos (Fig. 38). This species is known to be an early coloniser of new substrates and it is also prone to vacating its tube if disturbed (Kalugina, 1959). Laboratory and field observations at Rutland Water support this view. Larvae of this species are also known to migrate through the water column (Davies, 1973). This behaviour may result in large numbers of larvae occurring in the water column where they may be readily consumed by trout. If this were the case it would be expected that larvae would occur in stomachs for only a relatively short period as larvae are not adapted for feeding or swimming in the water column. Alternatively, if the low number of larvae observed in the benthos was in fact a result of sampling error then it would be expected that larvae would occur in trout stomachs over a longer period of time. Results indicate that the former hypothesis is more likely as 76% of the 8,319 E. albipennis larvae recorded in trout stomachs were found at the end of September 1977. Pedley and Jones (1978) recorded Endochironomus (species not recorded) regularly and abundantly in the benthos of Llyn Dwythwch, but larvae were not found in trout or salmon stomachs. Three possible explanations may account for this conflicting result; conditions required to stimulate the movement of larvae did not occur; sampling of stomachs did not include that period when larvae moved in the water column; or a different species with different behaviour patterns may have been involved.

In 1978 Psectrocladius was the dominant larval taxon consumed by either species of trout, and it was consumed in larger numbers than in 1977. This genus showed a large increase in

proportion to the total chironomid fauna (Fig. 33) and in actual numbers (Fig. 36) in 1978. Thus, the increased predation of this genus in 1978 may have been the result of larger numbers available to trout.

Data from 1977 indicate that larvae and pupae were eaten in different proportions by brown and rainbow trout. Rainbow trout were found to consume larger numbers of larvae, particularly the shallow water species, than brown trout. Pupae predominated in the diet of brown trout whilst larvae and pupae were found in approximately equal numbers in rainbow trout stomachs. This may reflect a difference in the feeding zones of the two trout species, rainbow trout feeding in shallow water and brown trout in deeper open water. This is a popularly held belief amongst anglers at Rutland Water who catch more brown trout by fishing in deep water from boats. In 1978 shallow water Psectrocladius larvae contributed 90% of the total chironomid larval diet of brown trout. 99% of these were found in stomachs sampled on 11th April 1978. Only 7 brown trout stomachs were obtained on this occasion and 2 did not contain Psectrocladius larvae. Three possibilities may explain these results: firstly, Psectrocladius underwent a similar migration as described for Endochironomus making the larvae available to brown trout feeding in deeper water; secondly, brown trout moved into shallow water to feed; thirdly, the sample of brown trout was too small to give an accurate estimate of the larvae consumed. This latter explanation is the most likely although the movement of larvae or fish cannot be discounted.

Seasonal changes in the number of larvae and pupae consumed by trout differed between the two years sampled. In August 1977 all stomachs sampled contained pupae. In 1978 the highest proportion of stomachs containing pupae occurred in May. Percentage number and percentage dry weight show a similar trend of high values in the latter part of the fishing season in 1977 (Fig. 60) but high values in the early part of the fishing season in 1978 (Fig. 62). This indicates that the main period of

chironomid emergence was different in the two years. This is supported by larval data for the two years (Figs. 34 to 41).

In 1977 and 1978 pupae contributed a greater proportion by dry weight to trout diet than larvae. This predominance of pupae in the diet has been recorded by several authors (Ball, 1961; Pedley and Jones, 1978). At Rutland Water chironomid larvae are abundant in the benthos throughout most of the year and pupae are numerous and accessible during periods of emergence. Together they made a significant contribution to the total biomass consumed by trout in both years sampled. The dry weight contribution of these organisms was depressed in 1977 by the large amounts of vegetation and earthworms present in the diet as a result of inundation of terrestrial habitats. There is no evidence that vegetation can provide any nutritional requirements of trout. It is likely that the presence of vegetation in trout stomachs is the result of it being taken in while fish feed on other items. In 1978 earthworms disappeared from trout diet and vegetation remains decreased from 29% by dry weight of the diet in 1977 to 7% in 1978. The proportion of larvae and pupae combined in the diet increased from 17% by dry weight in 1977 to 42% by dry weight in 1978.

CHAPTER 7

GENERAL DISCUSSION

Despite the large number of lowland, pump-storage reservoirs in Britain there appear to be few accounts of their ecology. The exceptions are studies on recreation (Saxton, 1969), trout fishery (Fleming-Jones, 1974; Fleming-Jones and Stent, 1975), water chemistry and algae (Toms *et al.*, 1975) at Grafham Water, and the Thames Valley reservoirs (see for example Mundie, 1975; Ridley, 1970; Steel, 1975). However, Rutland Water differs from these reservoirs in three main aspects, the development of the trout fishery, the morphometry of the reservoir basin and size (see Chapters 1 and 2).

The general aim of this study was to provide data on the benthic invertebrate populations of Rutland Water, with specific reference to the Chironomidae and to relate the findings to reservoir management procedures. An essentially holistic approach was adopted to provide a framework around which the development of benthic invertebrate populations could be discussed but also to provide a baseline for future research on the reservoir. This is the first comprehensive account of a large, lowland, eutrophic pump-storage reservoir managed as a trout fishery.

Techniques adopted

Several of the methods employed in this study are either new or are not generally used by other freshwater biologists. One of the major problems in freshwater biology is to produce accurate estimates of population densities of benthic invertebrates. In this study the problem was partly overcome by participating in a joint sampling programme. This enabled the chironomid fauna from 66 grab samples, taken monthly, to be obtained for analysis. This is a considerable increase on the numbers obtained by many other workers. To compensate for the increased sieving that this number of samples entails, a mesh size of 500µm was employed. This results in the underestimation of the smaller larvae that pass through the sieve (Jonasson, 1955).

Smaller mesh sizes greatly increase the sorting time and may still not provide accurate population estimates as it is known that many first and second instar larvae are planktonic (Davies, 1974).

A wide variety of benthic invertebrate sampling devices is used by freshwater biologists. In this study three mechanical grabs were evaluated. The first two, an Ekman grab and a Petersen grab, are widely used and the third is a modified van Veen grab specifically designed for use in reservoirs. The modified van Veen grab was found to be the most efficient in terms of the profile cut and ease of use.

Many investigators base their results on collections of chironomid larvae only. Considerable advantage can be gained, however, by collecting larvae, pupal exuviae and male adults. Collection of pupal exuviae permitted the construction of a more extensive species list and with considerable savings in time and effort. The exuviae also provide an alternative estimate of the relative abundance of species and of emergence periods. However, several sources of error are possible. The composition of the exuvial sample depends upon the length of time different exuvial species float and their rate of decomposition. In the river Chew, Wilson and Bright (1972) found exuviae had a half life of approximately two weeks in the spring and one week in the autumn. It is possible that the smaller and more delicate forms such as the Tanytarsini will be destroyed before the larger types such as the Chironomini, although no experimental evidence is available. Given the sampling interval employed at Rutland Water it is likely that each sample was representative of the species that had emerged since the previous sample. Adult males provide further information on the species present in the reservoir although some specimens may be collected that originated from other nearby aquatic habitats.

The collection of 66 grab samples per month over a several year period and the identification of chironomid larvae and other invertebrates

in each sample results in the accumulation of large amounts of data that are difficult to manage unless stored in a computer. In this study all data were stored on magnetic tape in a Burroughs 6700 computer and a statistical software package, SPSS (Statistical Package for the Social Sciences) was used for the analysis. Although designed for another discipline the package was found to be particularly useful for the data modifications, manipulations and analyses required in this study (Appendix A).

Reservoir Development

As was predicted from the data on the water supply rivers (Nene, Welland and Gwash) Rutland Water has become a eutrophic reservoir. Nutrient loadings, maximum winter nitrogen and phosphorus concentrations, summer chlorophyll-a concentrations and gross primary productivity are all typical of a eutrophic condition (Harper, 1978). The chironomid fauna has also been used to classify lakes and reservoirs according to their trophic status. Thienemann (1925) produced one of the earliest classifications and this has been modified and elaborated by a number of workers (for example Lundbeck, 1926; Berg, 1938; Brunden, 1958). Generally it is stated that Chironomus is characteristic of eutrophic lakes and Tanytarsus characteristic of oligotrophic lakes. Nursall (1952) and Paterson and Fernando (1970) have both recorded similar changes, from Chironomus dominated to Tanytarsus dominated chironomid fauna, in new impoundments. In both these cases, however, the initial eutrophic conditions were the result of the release of nutrients from flooded terrestrial vegetation, and the reservoirs reverted to a fundamentally oligotrophic state once the nutrient concentrations declined. At Rutland Water in the first three years of existence Chironomus, predominantly C. plumosus, was the numerically dominant chironomid species in the reservoir. However, in the fourth and fifth years Chironomus declined in abundance and Tanytarsus larvae predominated. The main species were T. bathophilus, T. gracilentus and T. lestagei (based on pupal exuviae and adult data, Tables 22 and 23). Nutrient concentrations and chlorophyll-a levels

were lower in the fourth and fifth years of the reservoir's existence although it would still be classified as eutrophic. In eutrophic Lake Myvatn, Iceland, Lindegaard and Jonasson (1979) found that T. gracilentus comprised 79% of the total benthos. Thus, as at Rutland Water, attempts to classify the trophic status of the water on the basis of identification of the chironomid fauna to the generic level may be misleading.

At Rutland Water two variables, climate and filling regime, have introduced complications into the sequence of ecological succession. Climatic conditions in the latter part of 1975 and the first half of 1976 resulted in the 'drought' conditions experienced in 1976. The reservoir water level had remained relatively steady for approximately 18 months (Fig. 9) and dense populations of benthic invertebrates developed. At the end of 1976 and the beginning of 1977, there was a rapid rise in water level, the result of high rainfall and the recommencement of pumping, which severely affected populations of littoral invertebrates. A large area of land was inundated and surviving populations 'diluted' throughout the reservoir. The Orthocladini for example were abundant during the summer of 1976 but following inundation were not recorded at all (Figs. 35 and 36).

The first three years of the reservoir's existence (1975, 1976, 1977) were dominated by marked fluctuations in various physiochemical factors. During periods of pumping river water into the reservoir, nutrient concentrations increased as nutrients were released from decomposing vegetation, and later decreased as nutrients were taken up by sediments and algae. These changes in physiochemical factors, thus, influence the size and composition of the phytoplankton community. This in turn is known to determine the changes and variations of various physical and chemical factors in the reservoir bottom, for example oxygen regime, alkalinity, pH (Jonasson, 1970). As phytoplankton are the main primary producers in the reservoir they influence directly or indirectly the composition of the benthic invertebrate fauna.

Phytoplankton as a primary producer is the major energy source for secondary production in large lakes and reservoirs. Annual gross production and seasonal changes in annual gross production are both important for the bottom fauna. The most thorough study of the relationships between physiochemical parameters, phytoplankton and chironomid populations is for Chironomus anthracinus populations of Lake Esrom, a Danish eutrophic lake (Jonasson, 1961, 1964, 1965). The ecology of this species of chironomid is similar to Chironomus plumosus, the dominant species in Rutland Water during the first three years of its existence.

Jonasson found that most of the spring peak of phytoplankton is consumed by C. anthracinus larvae after it had sedimented to the bottom. The larvae consequently show fast growth rates prior to emergence. During the summer period oxygen concentrations decline in the hypolimnion and the larvae appear to be unable to utilise the phytoplankton. After the summer period the autumn overturn enables warmer lake water, rich in oxygen and algal food, to reach the mud surface. Consequently larval growth is again rapid. During the rest of autumn and winter primary production is low and larval growth rate is also slow. It is likely that a similar sequence of events will occur at Rutland Water although the duration and area over which the reservoir stratifies is unknown. The general sequence of seasonal algal changes observed at Rutland Water (Fig. 24) are similar to those recorded in Lake Esrom (Jonasson, 1970). However, the year to year variations at Rutland Water are more marked due to the comparative immaturity of the system.

After an initial build-up in the number of C. plumosus larvae in a new reservoir there is a decline in numbers and a gradual replacement by a more diverse fauna (Nursall, 1952; Paterson and Fernando, 1970; Cantrell, 1975). At Rutland Water this decline began in 1977 and continued throughout 1978, the third and fourth years after the start of filling. A number of other Chironomini also showed a decline in numbers. Microtendipes increased in numbers, particularly in 1979. A number of factors are thought to contribute to these changes,

including interspecific competition (Cantrell, 1975) and changes in the substrate (McLachlan and McLachlan, 1976; McLachlan and Cantrell, 1976).

The formation of a sediment layer is an important feature in the development of new reservoirs (McLachlan and McLachlan, 1976). The processes of sediment formation are described by Brundin (1958) and Eltringham (1971). McLachlan and McLachlan (1976) describe a three-way interaction between water chemistry, sediment formation and mud dwelling fauna, which brings about the development of the mud habitat. Mechanical disturbance of the reservoir bottom by wave action and burrowing activity of animals releases ions into solution, which in turn cause precipitation of clay particles. Rearrangement of particle size is effected by the differential settling rates of suspended particles and the aggregation of particles caused by animal feeding and tube building behaviour. A relatively low rate of sedimentation is likely in Rutland Water since the stream inflow is small. In the early years of the reservoir marked sediment differences in different regions are likely. The central basin was flooded two years prior to the ends of the north- and south-arms and the relative development of the chironomid fauna in the two habitats reflects this difference (Fig. 44).

Modelling Aspects

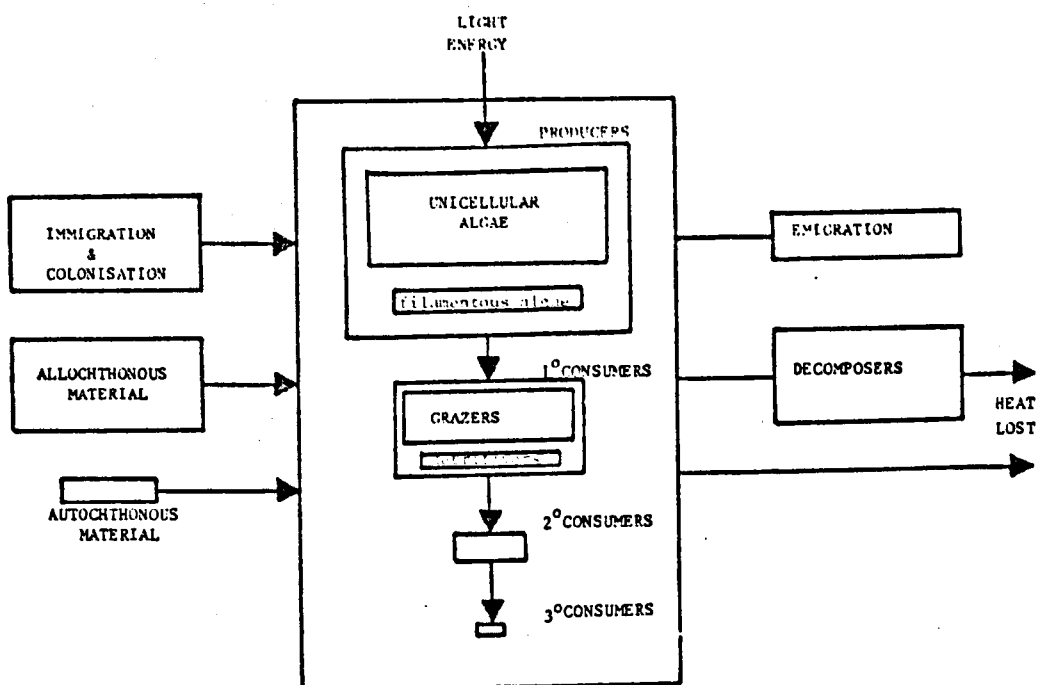
A number of authors have attempted to produce unifying theories of ecosystem development and Table 42 combines the characteristics of a developing ecosystem as described by Margalef (1968) and Odum (1969). Certain data are available from Rutland Water to test this model.

Major changes in energy flow between a newly formed reservoir and an established reservoir, based on data obtained in this study and other published data (MacArthur and Wilson, 1967; McLachlan, 1977), are shown in Figure 63. Production or respiration measurements were not made at Rutland Water and hence numerical values cannot be placed on the energy flows. In the early stages of development the rate of

Table 42: Model of ecosystem development based on data from Odum
(1969) and Margalef (1967, 1968)

	Immature Ecosystems	Mature Ecosystems
Production/biomass ratio	high	low
Production/respiration ratio	1	approaches 1
Net production	high	low
Food chains	short, linear, grazing	long, web-like, detritus
Biomass	low	high
Species diversity	low	high
Biochemical diversity	low	high
Organism size	small	large
Organism complexity	simple (uni- cellular)	complex (multi- cellular)
Population fluctuations	marked	weak
Population control	external	internal
Niche specialisation	broad	narrow
Life cycles	short (simple)	long (complex)
Allochthonous organic material	high	low
Nutrient exchange (org. to envir.)	rapid	slow
Mineral cycles	open	closed
Role of detritus in nutrient regeneration	unimportant	important
Interdependence of organisms	weak	strong
Resistance to perturbations	poor	good

a. IMMATURE SYSTEM (newly created reservoir)



b. MATURE SYSTEM (established reservoir)

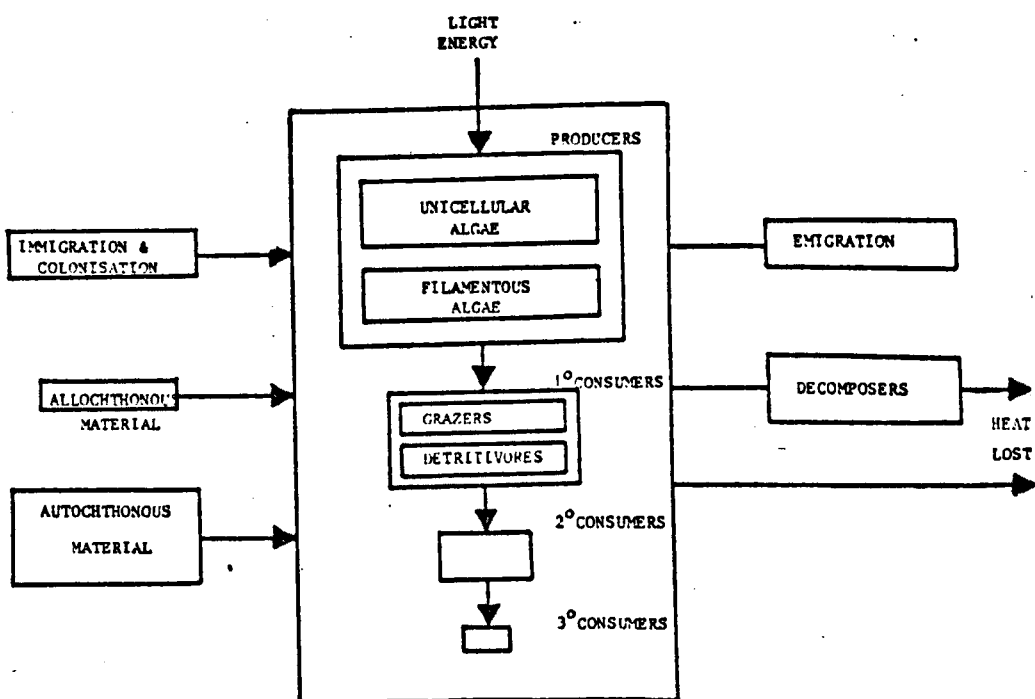


Fig. 63. Schematic diagram indicating some of the major changes in energy flow through a newly created and an established reservoir.

immigration is high whilst the rate of emigration is low. Typical extinction (emigration) and immigration curves for a developing system are given by MacArthur and Wilson (1963). McLachlan (1977) investigated the changing role of allochthonous and autochthonous organic material in a newly flooded lake and he concluded that mud dwelling animals were initially dependent on allochthonous organic material but later switched to autochthonous-based food chains. Initially the flooded terrestrial vegetation provides a large biomass upon which the decomposers can act and it is possible that the energy flow to the decomposers decreases as the system matures. In spring 1975, the start of filling, large blooms of small unicellular algae were observed at Rutland Water. Few filamentous algae were observed although this may have been the result of the rapid rise in water level. When the reservoir was nearly full and the water level stabilised, filamentous algae increased in abundance together with a few rooted macrophytes. Also observed at Rutland Water was the initial predominance of grazing organisms such as certain species of Orthocladinae larvae. Detritivores such as Asellus were initially restricted to areas of the flooded stream bed where presumably some detritus accumulations remained. Thus, grazing organisms predominate over detritivores in the early stages of impoundment. The actual changes in secondary and tertiary consumers in immature and mature ecosystems are unknown although intuitively they would be expected to depend upon the primary consumers and hence on the primary producers. At Rutland Water coarse fish populations were increasing in size during the study. The evidence of major changes in energy flow support the predicted change from grazing to detritus food chains in the model of a developing ecosystem (Fig. 63). Organism size and organism complexity aspects of the model (e.g. the early invasions of unicellular algae in early 1975, Fig. 22) are also supported by these data. To a lesser extent some of the nutrient cycling aspects of the model, such as changes from allochthonous organic material to autochthonous material, (Table 63) are also supported.

The biomass of organisms in new impoundments appears to increase rapidly and reach a peak after varying periods of time (Armitage, 1977). This peak is followed by a gradual decline although second peaks in biomass have been recorded by Armitage (1977) and others. The low biomass in an immature ecosystem and high biomass in a mature ecosystem, as predicted in the model (Table 63), thus depend on the time scale over which the observations are taken. In an immature ecosystem such as a new reservoir the biomass may in fact be higher than in a mature reservoir. Species diversity and population fluctuation aspects of the model appear correct for new reservoirs. Organism diversity increased at Rutland Water during the first four years of existence although diversity indices were not calculated. Marked population fluctuations were observed for a variety of taxa at Rutland Water and this supports the model in Table 63.

Despite the large amount of research that has been undertaken on a variety of developing ecosystems a number of the parameters of the model remain to be tested.

Results in relation to management

The management of water abstraction in lowland eutrophic reservoirs poses several problems that are mainly attributable to algal blooms (Ridley, 1970; Steel, 1972; Youngman, 1975). Many of the species recorded at Rutland Water are known to cause problems during water treatment, for example the blocking of filter beds by Scenedesmus, Stephanodiscus and Asterionella; colour, odour and taste problems caused by Cryptomonas and Microcystis. The latter species is also known to release substances toxic to fish (Gorham, 1964). Algal blooms may also be sufficiently severe to cause deoxygenation in the hypolimnion due to bacterial decomposition of dead cells. The anaerobic conditions produced cause chemical changes at the mud/water interface, for example the release of iron and manganese which taint and colour the water; the release of hydrogen sulphide; the release of phosphate and silica which are then available for further algal growth. The design features of Rutland Water, described in Chapter 2, were

intended to alleviate these problems. It was hypothesised that by directing inflowing water into the south-arm of the reservoir, high algal crops would deplete the water of nutrients before circulation into the north-arm (Water Research Association, 1971). Harper (1978) presents some evidence to suggest that differences in water quality do occur between the north-arm, south-arm and central basin but is uncertain as to the causative factors. Chemical data presented in this study suggest that there was little difference in surface water chemistry in the reservoir in 1978. It is known that spatial redistribution of algal populations can be brought about by wind induced water movements (George and Edwards, 1976; George and Heany, 1978) and in a relatively exposed reservoir such as Rutland Water this may be more important than local changes in algal populations brought about by nutrient and temperature differences.

As Harper (1978) states, the major design feature of Rutland Water is its versatility of operation. Water may be taken from the River Welland or the River Nene and pumped into the reservoir or alternatively be taken direct to the treatment works, bypassing the reservoir (Fig. 64). Two outlet points are located in different areas of the reservoir and each has the facility for abstracting water from different depths. Helixors provide the means of destroying vertical thermal stratification in the central basin and although the efficiency of the system was not fully tested during this study similar equipment installed in other reservoirs has indicated its value in artificial destratification (Symons, 1969). In relatively shallow exposed reservoirs such as Rutland Water (mean depth 10m, maximum depth 34m) periods of stratification may be of relatively short duration (Fig. 20) and occur in a limited area of the reservoir. This, together with the various options available for water abstraction, may negate the need for destratification equipment.

A knowledge of the ecology of chironomids may be of significance to the management of Rutland Water for three main reasons:-

- 1) The shape of the reservoir basin enabled design features to be instigated such that the two 'arms' and central basin could be

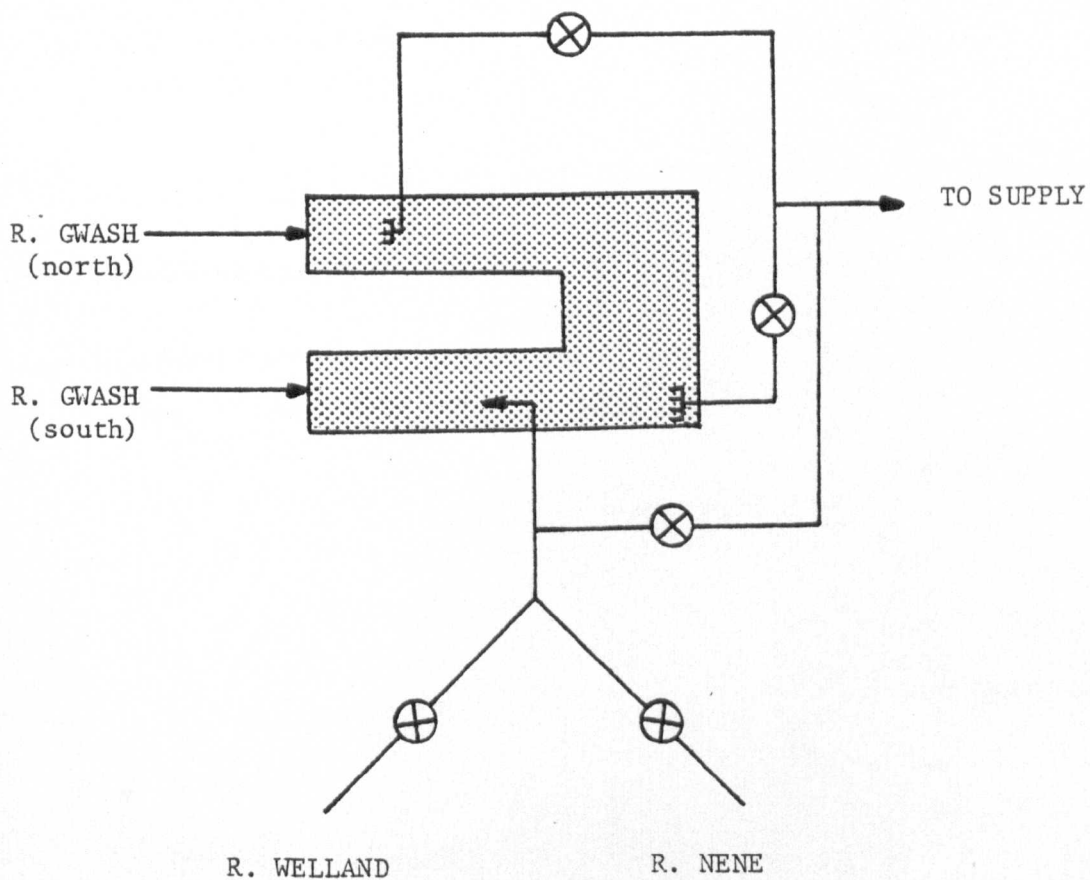



Fig. 64 Diagrammatic representation of water transfer options available at Rutland Water.  control points.

considered as separate units for water abstraction. Spatial and temporal variation in chironomid larval populations may reflect variations between these units.

- 2) Swarms of adult chironomids may be a nuisance to local residents as well as to fishermen and other visitors to the reservoir. Prediction of the months in which the problem will be most severe may enable preventative or curative measures to be taken.
- 3) Chironomid larvae and pupae form an important part of brown and rainbow trout diets. As the reservoir is managed as a sports fishery on a 'put and take' basis, it is generally desirable that stocking should be undertaken in such a way as to achieve maximum rates of growth and that the age structure and population size is matched to the available food resources. Alternatively the variables susceptible to manipulation, such as river water input, rate of abstraction, periods of helixor operation and to some extent nutrient inputs and sedimentation may be manipulated to promote appropriate chironomid populations.

Investigations of benthic macroinvertebrates revealed spatial and temporal changes in species composition and numbers. Variation in the numbers of Asellus and Gammarus between the western ends of the north- and south-arms was related to differences in substrate. The major difference between the second north-arm and second south-arm transect was in the proportion of Orthoclaadiinae larvae present (Fig. 44). The highest proportion of Orthoclaadiinae larvae was recorded from the second north-arm transect due to its shallow mean depth. This may not, however, be representative of the western ends of the two reservoir arms in general. Analysis of the similarity between the six transects, using Raabe's coefficient based on the dominant chironomid taxa, revealed no major differences between the north-arm and south-arm of the reservoir. The distribution of benthic invertebrates is likely to be influenced by a wide variety of environmental variables, for example substrate type, water quality, depth, seston formation, light penetration, oxygen concentrations, wind and wave action, as well as

biotic factors such as competition and predation. It is probable that physical differences between the two 'arms', rather than chemical differences, play a more important role in determining the spatial distributions of chironomid larvae in the reservoir.

The majority of chironomid species form aerial swarms of adult males (Lindeberg, 1964). These may be a nuisance to local inhabitants and reservoir visitors, particularly at dawn and dusk when most species emerge (Potter and Learner, 1974). Various methods have been employed to control chironomid populations and these may be divided into three categories: chemical, biological and environmental.

Applications of DDT and other chlorinated hydrocarbons have been used to control larvae (Flentjie, 1954, cited in Bruggemann, 1965) and have been suggested for the control of adults (see Grodhaus, 1963). However, these insecticides are known to have severe effects on other members of the freshwater community and chironomid populations may become resistant (Hunt and Bischoff, 1960). Biological methods have included the introduction of herbivorous fish to reduce algal growth upon which the larvae live and feed, and insectivorous fish to consume larvae and pupae (Bruggemann, 1965). Environmental manipulations have received little attention for the control of chironomids but may include: reduction of the trophic status of the water by removing nutrient inputs; mechanical removal of algae from margins; increasing the drawdown zone; maximising fetch so that eggs and larvae will be concentrated along one shoreline where they may be removed by other agents. A bioengineering approach was successfully employed by Allott and Lomax Ltd. and Thomas (1977) on a tropical lake in Nigeria to control mosquito larvae and the snail hosts of schistosomiasis.

At Rutland Water it may not be desirable to remove chironomid larvae and pupae as they form an important component of the trout diet; thus, control should be centered on the adult stage. Most species appear to have characteristic swarming sites and provided swarms are not disrupted by wind, the same species may use the same locations

each year (Lindeberg, 1964). If these sites can be described in terms of specific physical cues then alternative sites may be artificially provided and adults encouraged to swarm away from selected areas. Downes (1959) investigated the swarming flight and mating of Culicoides and induced the swarming of certain species over artificial markers. Chironomids are also known to be attracted to lights. Extensive use of light traps may reduce the number of adults swarming in selected areas. In both of these cases control would be considerably simplified if the species and its main emergence periods could be predicted in advance. However, data from this study cannot be used for this purpose as the reservoir underwent dramatic changes as the system developed and the equilibrium stage has not yet been reached.

Much controversy surrounds the use of eutrophic reservoirs as trout fisheries. Coarse fish (cyprinids and percids) are known to be better adapted to the prevailing conditions in a eutrophic water body than are game fish (salmonids and coregonids) (Larkin and Northcote, 1969). Hasler (1947) and Kriegsmann (1955) both provide evidence of lakes in which coarse fish populations have increased and fine fish populations have decreased as a result of eutrophication. However, a number of studies have shown an increase in growth rates of trout in artificially fertilised lakes (for example Smith, 1955; Munro, 1961). Oliver (1968) suggests that lowland eutrophic reservoirs can be successful trout fisheries if correctly managed.

The aims of management of a lowland reservoir trout fishery are not easily defined. The ultimate aim is to cater for the needs of fishermen and in such a way that fishermen are attracted to the reservoir in sufficient numbers to make the fishery viable. However, the needs of individual fishermen may vary considerably. At one extreme are those who prefer to catch fish regularly and easily irrespective of size and weight, whilst at the other extreme are those who prefer a challenge and often seek the larger specimen fish. Nevertheless, whatever the required stock density and age structure of the fish population it is generally desirable to make the maximum use of the

available natural food resources.

During the first two years of Rutland Water's existence the number of trout stocked ($250 \text{ ha}^{-1} \text{ yr}^{-1}$) was high compared to other lowland reservoirs (Crisp and Mann, 1977) although the stocking rate in terms of weight (1.3 kg ha^{-1}) was low. No estimates of the trout mortality are available during this period but the remaining fish grew well as a result of a population explosion of certain aquatic food organisms, mainly littoral crustaceans and chironomids, and the availability of terrestrial food, particularly earthworms (Warlow, pers. comm.). During this period of the reservoir's development it is difficult to determine seasonal trends in food organism abundance as a result of both the rapid successional changes in the fauna and the effects of water level rises. Trout were stocked from March to October 1975 and from March to May 1976 (Table 17) and it would be difficult to determine in which months trout should have been stocked in order to have the most abundant food supply.

In 1977 all 85,115 trout were stocked in the last six months of the year (Table 17) and were in the length range 20-32cm, a takeable size. Trout obtained for stomach analysis in 1977 had a mean length of 36cm and are, thus, likely to give a good indication of the diet of the stocked trout. Chironomid larvae had a comparatively small overwintering population in 1976/77 and larvae generally became more abundant in the second half of the year (Fig. 44). In April and May 1977 earthworms were abundant in trout diet as a result of the rise in water level at the beginning of the year (Fig. 9). Chironomid pupae became important in the diet, in terms of dry weight, in July 1977 and larvae gradually increased in proportion in the diet to a maximum of 16% (dry weight) in October. Thus, in terms of the chironomid component of the diet the first fish stocked in July 1977 had an abundant food supply of pupae whilst fish stocked in later months utilised the high population density of larvae.

In 1978 the reservoir was restocked with 54,680 trout in the length range 28-35cm, between April and July (Table 17), 77% of these

being stocked in April. Chironomid pupae constituted the most abundant food item consumed in April and May (66% and 81% respectively by dry weight). From the analysis of pupal exuviae, March to May was the main emergence period of chironomids in Rutland Water (Table 22). The population density of larvae was also high at this time although declining to a minimum in the summer months (Fig. 44). Thus, trout stocked at this time of year had a good chironomid food supply. In June, July and August the proportion, by dry weight, of larvae and pupae declined and Gammarus, Asellus and Lymnaea peregra increased. However, an index of stomach fullness calculated by Warlow (pers. comm.) indicated that stomachs contained less food than in the previous months. Trout stomachs analysed during these months contained low numbers of pupae and in fact no larvae were found in stomachs collected in September and October. Thus, fish stocked in these months had a poorer food supply and would, therefore, have slower rates of growth. Again longer term trends in chironomid populations cannot be predicted from data in the present study due to the rapid development of the reservoir and the complications arising from fluctuating water levels and climatic variations.

Provided the nuisance aspects of adult chironomids are not too great and can be tolerated or controlled then it may be beneficial to the fishery to promote chironomid populations as a food resource. At Rutland Water Procladius, Cricotopus, Psectrocladius and for a short period Endochironomus were the main larvae consumed by trout (Tables 33 and 37). Generally tubiculous larvae were not important in the diet. The free living, essentially littoral, larvae may be promoted by allowing the establishment of rooted macrophytes and benthic algae around the margins of the reservoir. At Rutland Water these are mechanically removed from most parts of the reservoir thereby reducing a valuable food resource. Fluctuations in the water level, which are accentuated in a pump storage reservoir, due to pumping and draw-downing, may also reduce populations of littoral chironomids.

A number of different pupal genera are consumed by trout at Rutland Water (Tables 36 and 38). These include the taxa with

tubicolous larvae that the fish do not consume. To promote these larvae may require increasing the nutrient loading of the water by artificial fertilisation. During the early stages of reservoir development populations of tubicolous larvae may also be promoted by increasing the rate of sediment formation. However, in all these examples it must be remembered that social, political and economic factors may impose constraints on the fishery management. These frequently overrule decisions based on ecological factors alone.

Further work

Three areas for possible future research are indicated from data in the present study. Firstly, wind driven water circulation patterns were omitted from the original design considerations of the reservoir. These are of particular interest with regard to the spatial distribution of algae and other organisms and the quality of water for abstraction. Investigation of the water circulation patterns, utilising physical models in a wind tunnel and on site observations, may enable predictive mathematical models of the water circulation patterns, periods of likely algal blooms and their spatial locations to be developed. High quality water could then be abstracted from the various outlet points without the need for constant reservoir or treatment plant monitoring.

Secondly, there appears to be a general dearth of autecological studies on the Chironomidae. This is particularly true for those species that occur in the littoral zones of lakes and reservoirs. The reasons for this neglect are the complexity of the littoral community and the difficulties of larval identification to the species level. The latter problem is at present being tackled by a number of workers (e.g. Cranston, pers. comm.; Pinder, pers. comm.) and correct identification, after rearing to the adult, is now possible for most British species. Work should concentrate initially on the numerically dominant species occurring in the community.

Thirdly, although chironomids play a major role in reservoir ecology, little field experimentation has been carried out to either

control or promote populations using environmental perturbations. Considerable progress is being made in the bioengineering approaches to the control of certain aquatic organisms, mainly those concerned with disease transmission (e.g. Allott & Lomax Ltd. and Thomas, 1979) but little work has been carried out on chironomids. Of particular value might be the redirection of swarming adult males by the use of artificial site markers. On the promotion side there is a need for more detailed information on the importance of chironomids in various fisheries and the integrated management of both fish stocks and their food organisms.

SUMMARY

1. The successional changes in benthic invertebrate populations in new reservoirs, with particular reference to the ecology of the Chironomidae, is reviewed.
2. The morphological and limnological features of Rutland Water, a pump storage reservoir, are described together with the geology and meteorology of the area.
3. A modified van Veen grab for sampling benthic invertebrates is described and its efficiency is compared with the Ekman and Petersen grabs. Air/ground trials, parallel sampling trials and underwater observations were made. The van Veen and Ekman grabs were used in this study.
4. The number of sampling units required to obtain reliable estimates of the population density was investigated. Participation in a joint sampling programme with Leicester University enabled the chironomid larvae from between twenty and sixty-six grab samples to be obtained each month for analysis.
5. Further information on the chironomid species composition and relative abundance was obtained by collection of pupal exuviae from the reservoir margins and collection of swarming adult males by sweep netting. Species identification of some larvae was confirmed by rearing to the adult stage.
6. Chironomids in brown and rainbow trout diets was investigated by the collection of stomachs of fish caught by boat or bank fishermen.
7. Data provided by the Anglian Water Authority were analysed and used to describe the physical and chemical features of the supply rivers (Nene and Welland); the water chemistry, phytoplankton and trout fishery of the reservoir.

8. During the first three years of the reservoir (1975-1977) major changes in nitrate and phosphate concentrations were found to coincide with periods of filling. The increase in concentration of these nutrients during filling reflects both the input of nutrient rich river water and the release of nutrients from the inundated terrestrial vegetation. No pronounced seasonal fluctuations in nutrient concentrations were observed and the concentration declined steadily throughout 1978, a period during which the water level rose by a comparatively small amount.
9. Design features were implemented to make the south-arm the most nutrient rich area of the reservoir. However, no significant spatial differences in water chemistry were observed in 1978. During each year of the study a thermocline began to develop in the central basin of the reservoir at the beginning of June and lasted for varying periods of time.
10. Chlorophyll-a concentrations were particularly high at the beginning of 1975 but declined later in the year. In the following three years concentrations showed seasonal fluctuations similar to other eutrophic reservoirs. The seasonal succession of phytoplankton, after 1975, was also similar to that of other eutrophic reservoirs.
11. Several taxa including Hydra and Stylaria lacustris showed rapid population growth and decline in the first few years of the reservoir's development. Gammarus pulex, Asellus aquaticus, Asellus meridianus, Lymnaea peregra and several Hirudinea species were abundant and were recorded regularly from the end of 1977. Initially Asellus spp. were restricted to areas of detritus deposits in the impounded stream bed. Later they were found to spread to the reservoir margins. Ephemeroptera, Coleoptera and Trichoptera all showed slow population growth. Terrestrial organisms, particularly earthworms, were recorded in grab samples after periods of water level rise.

12. Orthocladiinae larvae were particularly abundant in the summer 1976, probably as a result of the warm summer and extensive mats of benthic algae that grew in the shallow water. This sub-family was not recorded in grab samples for a period of five months after a rapid rise in water level at the end of 1976. Chironomus plumosus and Polypedilum nubeculosum, species with tubiculous larvae occurring at all water depths, were abundant in the latter half of 1976. In 1977 and 1978 the major changes in the chironomid community were a decline in the density of C. plumosus and P. nubeculosum larvae and an increase in density of Tanytarsus species.
13. Collections of pupal exuviae in 1978 were found to provide a more extensive species list than larval or adult collections, with less expenditure in time and effort. Although exuviae collections did not provide quantitative data they did provide additional data on the relative abundance of those species more easily separated as exuviae than as larvae; for example, Psectrocladius sordidellus and Psectrocladius barbimanus.
14. The spatial dispersion of chironomid populations were mathematically described using Taylor's Power Law. Using this and other indices of dispersion, populations were found to be contagiously distributed throughout the reservoir, within different depth zones and at different times of year. Combining samples from all parts of the reservoir, populations generally became more clumped at lower population densities. This is probably a reflection of habitat variation as samples collected from one site (i.e. one substrate) showed these populations to be more randomly distributed.
15. No clear spatial differences in chironomid populations were found between the two arms of the reservoir. With regard to the dominant chironomid species composition the transects were found to change in their similarity with each other each month. The highest population densities were recorded at the western ends of the two arms and the lowest population densities in the central basin.

This is likely to be predominantly a reflection of the mean depth of each of the transects sampled.

16. Chironomid species composition, seasonal population changes and depth distributions were investigated and compared with published data on other eutrophic reservoirs. Generally trends were similar although results at Rutland Water were influenced by climate variation and by the filling regime.
17. Orthocladiinae and Tanypodinae larvae were found to be more abundant in trout stomachs than the tubiculous Chironominae larvae. Numbers of larvae were higher in stomachs in July and August 1977 than in other months. In 1978 numbers were highest in April. Chironomid pupae contributed an important proportion to the diet of trout during periods of emergence. Few adult chironomids were found in trout stomachs.
18. Rainbow trout consumed significantly larger numbers of shallow water chironomid larvae than did brown trout. Rainbow trout thus appear to feed in shallower water than brown trout.
19. The proportion of different species of larvae in trout diets was not directly related to their abundance in the benthos. Tanytarsus spp. and Polypedilum nubeculosum, although abundant in the benthic samples, only occurred in low numbers in trout stomachs. The reverse was true for Endochironomus albipennis. This species occurred in considerable numbers in trout stomachs on one sampling occasion in October 1977. Various hypotheses were put forward to explain this result. It is likely that individual species behaviour is more important than numerical abundance in determining the overall contribution to trout diet.
20. Results are discussed in relation to management practices at the reservoir. It was suggested that the observed spatial differences in phytoplankton populations were more likely to be the result of wind induced water circulation patterns than spatial

differences in physico-chemical parameters. This may not be true during periods of pumping nutrient rich river water into the south-arm. Chironomid populations were not found to reflect any differences in water quality between the two arms of the reservoir.

21. Due to the importance of chironomids in trout diet stocking should be undertaken in such a way as to make the maximum use of the available food resources. It may be beneficial to the fishery to promote larval populations. Various suggestions have been put forward including cessation of ^{the} practice of mechanical removal of benthic algae and macrophytes from the margins.
22. If chironomid adults become a nuisance to local residents or reservoir visitors then various control strategies should be considered. Suggestions have been made.

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Appendix A

The Application of a Statistical Package for the Social Sciences to an Ecological Survey of Benthic Fauna

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ABSTRACT

SPSS is applied to data obtained from an ecological survey of the benthic fauna in a new reservoir. Three program examples are described together with the output obtained. Program 1 computes the mean, standard error, standard deviation, variance, kurtosis, skewness, range, maximum, minimum and sum of a series of data. Program 2 illustrates one adaptation of an SPSS point plotting facility. Program 3 computes one of several correlation coefficients available.

INTRODUCTION

SPSS* (statistical package for the social sciences) is a computer program package extensively used for the analysis of social science data. Due to its ease of use and the large number of statistical computations available, it is finding increasing use in other disciplines. Data obtained from an ecological survey of a newly created reservoir were analysed using SPSS. The following program examples are intended to inform the reader of the facilities SPSS offers. The paper does not contain detailed instructions for the use of SPSS; these are provided in the SPSS manuals (Klecka, Nie and Hadlai Hull, 1975; Nie et al, 1975).

*This package is an item of proprietary software, the Licensor being SPSS Inc., 444 North Michigan Avenue, Suite 3300, Chicago, Illinois 60611, U.S.A.

METHODS

The survey

The aim of the benthic invertebrate survey was to determine the pattern of development of the fauna in the reservoir. Larvae of the midge family Chironomidae were the numerically dominant benthic invertebrates and the first step was to obtain reliable estimates of their density together with their temporal and spatial distribution patterns.

Monthly samples were obtained from the reservoir using a standard Ekman grab, sampling area 227 cm^2 and a modified van Veen grab, sampling area 325 cm^2 . Ten or twelve grab samples were taken along each of six transects, the actual number depending on the transect length. Ecological surveys are frequently of this type with a number of samples being taken at each station or transect; hence the type of statistical analysis described may be appropriate for a range of different survey data.

Arrangement of data for input to SPSS

Instructions and data are given to SPSS on computer cards. The computer cards can be divided into two groups: "control cards" define the structure of the data and state which statistical procedures are required and "data cards" record the actual results of the survey (Fig. 1).

Control Cards

SPSS control cards are composed of two parts or fields. The "control field" (Fig. 1) occupies columns 1-15 on the card and contains a unique control word or set of words which informs SPSS of the specification that will follow so that the proper procedures can be called to act upon the information on the card. The "specification field" occupies columns 16-80. Here the user supplies the system with parameters, labels and/or instructions required to perform the function indicated by the control field.

Control cards can be divided into two groups: "data definition cards" that define the structure of the data to be analysed and "procedure cards" that request the type of statistical analysis (Fig. 1). A complete list of statistical analyses available with SPSS is provided in Appendix 1.

Data Cards

In this survey a grab sample is the basic unit of analysis and is referred to as a "data case". Nineteen variables are recorded in the data case. The data relevant to each data case are recorded in numerically coded form on a single line of a data sheet (Fig. 2). The columns of the data sheet are occupied by the nineteen variables that apply to the data case. Table 1 shows the column(s) that each variable occupies, the SPSS variable names and their descriptions and codes. The first six letters of each taxon of chironomid were used as variable names for easy recognition. A data card is punched from each line of the data sheet, i.e. there is a card for each data case (Fig. 3). In surveys where a large number of variables are present a data case may consist of several lines on the data sheet and hence several punched cards.

Data management facilities and program examples

All the information identifying the variables plus the data themselves are stored in the computer on a tape or disc, referred to as a computer file. The survey data, for convenience labelled CHIRSTUD (chironomid study), were divided into subfiles each containing data from one transect on one sampling data. This facility for subdivision is a feature of SPSS and has the advantage that statistical procedures may be repeated on any individual subfile, or groups of subfiles requested, with the minimum of program alteration. For instance, an analysis of temporal distributions in this study may require that the results from the six

transects be combined for each month's samples; alternatively an analysis of spatial distributions may require that each transect be considered separately but all the months combined. Individual data cases or complete subfiles of data may be added each time the file is accessed. In the survey this feature was found to be particularly useful in updating the file after each month's samples had been collected.

Example program 1

This program computes a series of statistics which frequently form the basis of ecological surveys. The SPSS program section is followed by a description of each step and the output containing the statistics.

Program

	CONTROL FIELD	SPECIFICATION FIELD
1	RUN NAME	EXAMPLE TASKS FROM FILE CHIRSTUD
2	GET FILE	CHIRSTUD
3	TASK NAME	BASIC STATISTICS
4	COMMENT.	EXAMPLE OF THE RETRIEVAL OF A GROUP OF SUBFILES AND THE REQUESTING OF STATISTICS FOR FOUR VARIABLES. THE VARIABLE PROCLA IS MULTIPLIED BY 44 TO CALCULATE THE NUMBER OF LARVAE PER METRE SQUARE. ALL OTHER STATISTICS ARE FOR LARVAE PER GRAB.
5	RUN SUBFILES COMMENT	(JU16,JU26,JU36) SUBFILE NAMES ARE MADE UP AS FOLLOWS: THE FIRST TWO LETTERS NAME THE MONTH THE FIRST NUMBER IS THE CODE FOR THE TRANSECT THE LAST NUMBER IDENTIFIES THE YEAR FOR EXAMPLE JU16 JU=JUNE 1 =DAM TRANSECT 6 =1976
6	*COMPUTE	PROCLA=PROCLA*44
7	CONDESCRIPTIVE	PROCLA,CHIRON TO ENDOCH
8	OPTIONS	1
9	STATISTICS	ALL

Steps explained

- 1 These control words enable the user to include any message in the specification field which identifies the run. This message is printed at the top of each page of output generated by the run.
- 2 This accesses a file, named "CHIRSTUD". The file was created, and the data defined using the data definition cards given in Fig. 1.
- 3 These control words enable the user to identify specific tasks within a run. The message in the specification field is printed below the run label on the top of each page of output to which it applies.
- 4 Comments may be placed anywhere appropriate in the control-card deck by the use of this control word. These comments are printed with the other control cards in the output. Control cards 1, 3 and 4 act merely as labels to identify the output.
- 5 These are mnemonics referring to subfiles created by the user. The parenthesis is required by SPSS so that the data from these three subfiles are processed together.
- 6 Here each value of "PROCLA" (Genus Procladius) will be multiplied by 44 and relabelled with the same name. The "*" before "COMPUTE" enables the user to make only temporary data modification, i.e. the new value of "PROCLA" will be used in next task only. The old value of "PROCLA" will be retained in the file and may be used on any subsequent statistical tasks.
- 7 This control word is used to request an SPSS subprogram that calculates certain statistics (Fig. 4). The "TO" notation enables all variables between and including the two either side of it to be processed (Table 1). The statistics for "PROCLA", "CHIRON", "CRYPTO" and "ENDOCH" will be computed.

- 8 Each statistical subprogram has several options associated with it. "OPTIONS 1" IN THIS CASE informs SPSS that all grab samples in which there was a zero value, for any of the variables, should be included in the calculation. Other "OPTIONS" available with the subprogram include computation of Z-scores and the outputting of a reference dictionary for the page locations of variables.
- 9 This control word and specification requests "ALL" the statistics available with the CONDESCRIPTIVE subprogram (Fig. 4). Each statistic is assigned a number by SPSS so that the user is able to select only those required, e.g. the statement "STATISTICS 1,2" would request only the mean and standard error.

Example program 2

This example is an adaptation of one of the SPSS subprograms. The scattergram produces a picture representing the relationship between two variables. The statistics available define a straight line that best approximates the pattern of the points, a simple regression analysis. In this example the depth of each grab sample is plotted against the number of one genus of chironomid larva in each grab. SPSS has produced a depth distribution for the larvae of the genus *Psectrocladius* (Fig. 5).

Program

	TASK NAME	SCATTER DIAGRAM
	COMMENT	THE NUMBER OF PSECTROCLADIUS LARVAE PER GRAB IS PLOTTED AGAINST DEPTH SAMPLED. THE OPTIONS CARD PRODUCES AUTOMATIC SCALING.
1	RUN SUBFILES	ALL
2	SCATTERGRAM	DEPTHS WITH PSECTRO
3	OPTIONS	7
4		

Steps explained

- 1 All the subfiles present in the file CHIRSTUD are to be run together. Alternatively any set of subfiles may have been requested, as in Example 1. If a statistical procedure is to be repeated separately on every subfile the control word "EACH" would be used instead of "ALL".
- 2 This is the control word used to produce the scatter diagram.
- 3 This "OPTIONS" card produces automatic scaling of the axes, i.e. the maximum and minimum values of each variable supplied in the data are the limits of the axes and the intervals are such that the whole graph can be drawn on one page of printed output. Other options available with this subprogram are described in the manual (Nie; op.cit.).
- 4 No statistics were required on the scattergram plot, so the statistics card was omitted.

Example program 3

This is one example from the wide range of statistics available with SPSS. The correlation analysis was used in the survey for determining the relationship between the occurrence of pairs of genera. The correlation coefficient, the number of cases (= number of grab samples) and the level of significance for each pair of variables are given (Fig. 6).

Program

	RUN SUBFILES	ALL
	TASK NAME	CORRELATION ANALYSIS
	COMMENT	EXAMPLE OF THE SELECTION OF CERTAIN
		SAMPLES, COMPUTING THE LOGARITHM OF THE
		REQUIRED VARIABLES AND CALCULATION OF
		CORRELATION COEFFICIENTS
1	*SELECT IF	(TRANNO GE 5)
2	*COMPUTE	PROCLA=LN(PROCLA)
	*COMPUTE	CRICOT=LN(CRICOT)
	*COMPUTE	ORTHOC=LN(ORTHOC)
	*COMPUTE	PSECTR=LN(PSECTR)
	*COMPUTE	CORYNO=LN(CORYNO)
	*COMPUTE	CHIRON=LN(CHIRON)
3	PEARSON CORR	PROCLA TO CHIRON
4	OPTIONS	1

Steps explained

- 1 This is a temporary data selection card. All data cases are run but only those with a transect number greater than 5 will be selected and used in the calculation.
- 2 A temporary COMPUTE card that calculates the natural logarithm of the variable PROCLA and assigns it to the same name. A new name may be assigned to the calculated figure if required, e.g.
NEWPROCL=LN(PROCLA).
- 3 The Pearson product-moment correlation statistic is requested. The TO notation requests a correlation coefficient for all the variables from PROCLA to CHIRON. Correlations between only two variables may be obtained using the statement PROCLA WITH CHIRON.
- 4 This OPTIONS card includes in the calculation all cases with zero values for the variables. A number of other options and statistics are available with this subprogram. Various other correlation coefficients are also available (Appendix 1).

Literature Cited

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Appendix 1

Statistics available with SPSS. Each of these subprograms has certain procedure cards associated with it; see for example Fig. 1.

AGGREGATE	- Aggregates subpopulation statistics
ANOVA	- Performs analysis of variance for factorial designs
BREAKDOWN	- Describes subpopulations and provides a one-way analysis of variance and test of linearity
CANCORR	- Performs canonical correlation
CONDESCRIPTIVE	- Provides descriptive statistics for variables
CROSSTABS	- Crosstabulates variables optionally controlling for other variables
DISCRIMINANT	- Performs multiple discriminate analyses
FACTOR	- Performs five different types of factor analysis
FREQUENCIES	- Provides frequency tables and descriptive statistics for variables
GUTTMAN/SCALE	- Performs scalagram analysis
NONPARR CORR	- Calculates Spearman or Kendall correlations
ONEWAY	- Performs one-way analysis of variance
PARTIAL CORR	- Calculates partial-correlation coefficients
PEARSON CORR	- Calculates Pearson product-moment correlations

- REGRESSION - Performs simple and multiple regressions
- SCATTERGRAM - Produces bivariate plots, Pearson's R, intercept and slope coefficients
- T-TEST - Computes student's t and probability levels for independent or paired samples

Acknowledgements

We would like to thank Leicester Polytechnic Computer Centre for the use of their facilities.

- Fig. I Basic SPSS instructions required for a program run. Only examples of control fields are included. Examples of specification fields for procedure cards are provided in the three examples discussed in the text.
- Fig. II Data sheet or coding form used to record survey data prior to punching onto computer cards. Data from three grab samples are shown. The variables and their locations are shown in Table I.
- Fig. III Data, as shown in Fig. I, punched onto computer cards.
- Fig. IV Output from Program Example 1. The date the program was run and the file creation data are also shown.
- Fig. V Output from Program Example 2. Single data points are represented by an asterisk (*). If two through to eight cases fall in the same position the actual number of cases is written. Nine or more cases are represented by the number 9.
- Fig. VI Output from Program Example 3. The subfile list indicates that all subfiles were run, but of these only 24 with a transect number greater than five were used in the calculation. The correlation, number of cases and significance are shown.
- Table I Codebook for the chironomid study.

CONTROL FIELD
(COLUMNS 1-15)

SPECIFICATION FIELD
(COLUMNS 16-80)

control cards	data definition cards	RUN NAME								
		DATA LIST								
		INPUT MEDIUM								
		N OF CASES								
		MISSING VALUES								
		VAR LABELS								
		VALUE LABELS								
	procedure cards	TASK NAME								
		CONDESCRIPTIVE								
		OPTIONS								
STATISTICS										
		READ INPUT DATA								
data cards		31 876 1 3		3 2 132 24 6						
		31 876 2 3		2 3 3 43 25 2						
		31 876 3 5		7 4				2		
control card		FINISH								

CODING FORM

NAME	A.E. BROWN	SCHOOL	LIFE SCIENCES	PAGE	1	OF	12	PAGES
USER CODE	BC4DAS1	EXT.	2206	DATE	8	4	73	

[illegible]

EXAMPLE TASKS FROM FILE CHIRSTUD
BASIC STATISTICS
FILE CHIRSTUD (CREATION DATE = 02/23/79) STUDY OF LARVAL CHIRONOMIDAE IN RUTLAND WATER
SUBFILE JUI6 DC16 JUI6 DE16 FE17 SC17 OC17 NO17 JAI8 MA10
AP18 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6
FE38 MA28 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6
JAI8 JAI8 JAI8 JAI8 JAI8 JAI8 JAI8 JAI8 JAI8 JAI8
DC57 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6
AUG7 SE67 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6 JUI6

VARIABLE PROCLA GENUS PROCLADIUS
MEAN 315.685
VARIANCE 467730.789
RANGE 4408.000
SUM 224136.000
VALID OBSERVATIONS - 710
MISSING OBSERVATIONS - 0

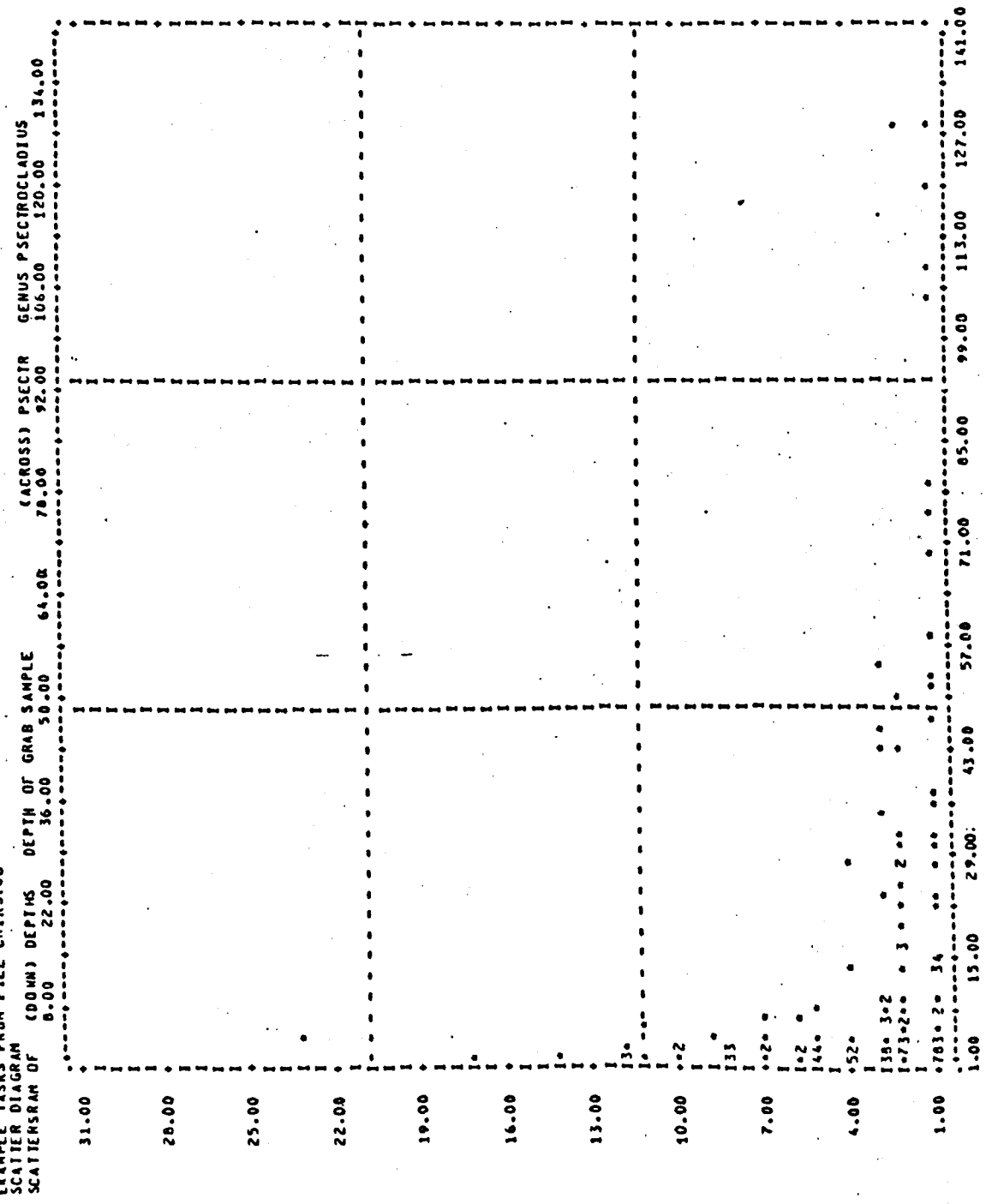
VARIABLE CHIRON GENUS CHIRONOMUS
MEAN 6.293
VARIANCE 216.303
RANGE 173.000
SUM 4472.000
VALID OBSERVATIONS - 710
MISSING OBSERVATIONS - 0

VARIABLE CRYPTO GENUS CRYPTOCHIRONOMUS
MEAN 0.317
VARIANCE 3.971
RANGE 29.000
SUM 225.000
VALID OBSERVATIONS - 710
MISSING OBSERVATIONS - 0

VARIABLE ENDOCH GENUS ENDOCHIRONOMUS
MEAN 0.662
VARIANCE 4.904
RANGE 35.000
SUM 470.000
VALID OBSERVATIONS - 710
MISSING OBSERVATIONS - 0

STD DEV 685.369
SKEWNESS 3.267
MAXIMUM 4488.000
STD DEV 14.710
SKEWNESS 6.304
MAXIMUM 173.000
STD DEV 1.993
SKEWNESS 10.844
MAXIMUM 29.000
STD DEV 2.214
SKEWNESS 7.712
MAXIMUM 35.000

EXAMPLE TASKS FROM FILE CHIRSTUD



Column(s)	SPSS variable names	Variable descriptions and codes
1- 4	SEQNOS	Sequence numbers. These identify individual cards but are excluded from programs.
7-11	SADATE	Sampling date (cols. 7 and 8 = day/cols. 9 and 10 = month/col. 11 = year)
12	TRANNO	Transect number in reservoir, numbers 1-6 are the codes that identify each transect
13-14	GRABNO	Grab number in transect (1 to 99)
15-16	DEPTHS	Depth of water in which grab sample was taken (1 to 99)
17-20	SAMPWT	Weight of grab sample (1 to 9999)
21-23	PROCLA	No. of larvae of Genus Procladius (max. value 999)
24-26	CRICOT	No. of larvae of Genus Cricotopus (max. value 999)
27-29	ORTHOC	No. of larvae of Genus Orthocladius (max. value 999)
30-32	PSECTR	No. of larvae of Genus Psectrocladius (max. value 999)
33-35	CORYNO	No. of larvae of Genus Corynoneura (max. value 999)
36-38	CHIRON	No. of larvae of Genus Chironomus (max. value 999)
39-41	CRYPTO	No. of larvae of Genus Cryptochironomus (max. value 999)
42-44	ENDOCH	No. of larvae of Genus Endochironomus (max. value 999)
45-47	GLYPTO	No. of larvae of Genus Glyptotendipes (max. value 999)
48-50	MICROT	No. of larvae of Genus Microtendipes (max. value 999)
51-53	POLYPE	No. of larvae of Genus Polypedilum (max. value 999)
54-56	TANYTA	No. of larvae of Tribe Tanytarsini (max. value 999)
57-59	PENTAN	No. of larvae of Tribe Pentaneurini (max. value 999)

Second South-Arm Transect

Grab Numbers

	1	2	3	4	5	6	7	8	9	10
23.10.78										
Mollusca				7		1	1			2
Oligochaeta	218	6		1	24	5	30	20	50	
Hirudinea	1								4	
Asellus			5	22	2	52	1	9		
Gammarus	8		43	6		7	14	19	4	41
Trichoptera			1			1	2			
20.11.78										
Mollusca				2	1			3		
Oligochaeta	2	14		2	7	1	1	4		
Hirudinea		3			1	1		2		
Asellus		4		1	6	1	2	15		
Gammarus	5	1	15	10		3	1	7	31	
14.12.78										
Mollusca			1	2			1	22	4	
Oligochaeta	4	14	3		18	5	1		12	
Hirudinea		6	1		1	3		2		
Asellus		16	1	1	7	12	7	8	9	
Gammarus	31	9	20	4	3	2	17	18	10	1
Trichoptera			1							
25.1.79										
Mollusca			1					7	3	
Oligochaeta		29	29		4	40	10	26	16	
Hirudinea						1	1	1		
Asellus		7	5		5	5	4	1	5	
Gammarus	7	17		1		7	3		56	
Trichoptera						2				
19.3.79										
Mollusca	3			2					1	
Oligochaeta			8	23	2	6	1		36	
Hirudinea						1		1		
Asellus			1				5	7	2	
Gammarus	9	4	4		1	2	2	3	19	1
19.4.79										
Mollusca						1		3	1	
Oligochaeta	3	19	7	2	39	33	13		36	
Hirudinea	2				2			2	2	1
Asellus		4			12	6		2		
Gammarus	25	1	1	5	1	4	1	9	16	10
Trichoptera						1				
Other Diptera			1							

(T = Terrestrial)	Second North-Arm Transect									
	Grab Numbers									
	1	2	3	4	5	6	7	8	9	10
12.5.77										
Oligochaeta	7	10	10						6	3
Oligochaeta (T)		1	2							
Gammarus										11
Tipulidae (T)		1								
26.5.77										
Oligochaeta	1					4		7	2	
Hirudinea									1	
Tipulidae (T)							2			
20.6.77										
Oligochaeta	54	10		7	4	53	7	3	24	27
Oligochaeta (T)		1	1							
Hirudinea		1			11					
Asellus					89					
Corixidae			1							
Tipulidae (T)		1								
Ceratopogonidae	1									
11.7.77										
Hydra	3									
Oligochaeta	9	47		52	11	82	5	115	153	120
Oligochaeta (T)	1									
Hirudinea						1				
Gammarus								1		
31.8.77										
Mollusca							1			
Oligochaeta	30	43	34				2		8	
Asellus		1			3					
Gammarus						1				
Ephemeroptera	1									
Corixidae		1	1							
Ceratopogonidae		1								
26.9.77										
Mollusca						1	5	1		
Oligochaeta	114						2	2	39	
Hirudinea					1				1	
Asellus	5				30	5	1	11	4	8
Gammarus				1		8	21	23	4	2
Ephemeroptera	2								1	
Corixidae	7								4	
Ceratopogonidae									1	
24.10.77										
Oligochaeta			11	5		1			6	11
Asellus				25	29	2	3	2	2	6
Gammarus				1		1	5	21	86	4

Second North-Arm Transect										
Grab Numbers										
	1	2	3	4	5	6	7	8	9	10
29.11.77										
Oligochaeta					4				16	5
Asellus	2				1	8	7		1	
Gammarus						4	1	4		
Ceratopogonidae	1									
16.1.78										
Oligochaeta	1			1			1	5		
Hirudinea				1						
Asellus	1	1		131	11	11	3	10		
Gammarus					3	9	1			1
Tipulidae (T)										14
28.2.78										
Oligochaeta	2			1				5		1
Asellus			95		6	3	13	5		
Gammarus			58		1	19	2	1	1	
Trichoptera			1	1						
Tipulidae (T)	7									1
Other Diptera	9								1	53
16.3.78										
Oligochaeta		3		1				1	5	2
Asellus		1			3	6	5	16		
Gammarus				4	2	8	6	1		
Tipulidae (T)	2	1								2
Ceratopogonidae		1								
Other Diptera	1			1					3	11
12.4.78										
Tricladidae					2					
Mollusca							1			
Oligochaeta			1							1
Hirudinea					1					
Asellus				28	129	14	10	9		
Gammarus		1		5		5	7	4	2	
Trichoptera										1
Other Diptera	1									4
17.5.78										
Oligochaeta	1									
Hirudinea	1									
Asellus			16	39	29	9	1	4		
Gammarus			4	1		4				3
Tipulidae	1									
13.6.78										
Oligochaeta	40			1		3			3	16
Hirudinea						1				
Asellus				3	6	31	25		9	
Gammarus					4		9			

Second North-Arm Transect

Grab Numbers

	1	2	3	4	5	6	7	8	9	10
10.7.78										
Tricladida				25	5					
Mollusca			1		1			1	2	
Oligochaeta	128	4	2	8	1		1			94
Oligochaeta (T)	4									
Hirudinea			1	4	3	3				
Asellus	40	5	172	224	54	19	112	347	14	4
Gammarus	4		3				6	22		16
17.8.78										
Mollusca	8						1			
Oligochaeta	4	1		1	1					
Hirudinea	4		7	1	1		2	1	2	
Asellus	80		230	5	5	3	13	114	171	3
Gammarus			31			2	15	15	26	40
19.9.78										
Mollusca	2						1			4
Oligochaeta					6		2			
Hirudinea	6		2	6	3	1			1	
Asellus	10	11	1	46	8	4	1	182	2	105
Gammarus				4	1	1	2	102	1	118
Ephemeroptera										3
Trichoptera	1									21
23.10.78										
Tricladida			2	1						
Mollusca	5				2	1			7	
Oligochaeta	61	2		1	13		1		2	108
Hirudinea		14	29	4	2		1		2	
Asellus	38	375	815	88	5	1	90	501	364	
Gammarus	6	11	324	2		11	16	144	56	136
Corixidae										4
Ephemeroptera									2	
Trichoptera	10								6	64
20.11.78										
Mollusca	3								6	1
Oligochaeta	23			327						
Hirudinea		4		27					1	
Asellus	32	7	1	13	2	3	85	254	80	2
Gammarus	24	2	18		9	19	7	87	39	14
Trichoptera	24	1	1							
14.12.78										
Mollusca									1	
Oligochaeta	5			37	14	3			1	
Hirudinea	4		3	1			1		3	
Asellus	7	19	256	43	16	4	1	410	69	
Gammarus	5	6	1	1	1		1	86	31	23
Trichoptera		1								

Grab Numbers

[illegible]

Date: 2.6.76

Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
SOUTH-ARM	1			168	10	109	4	4				.4	51
	2			107	3	70	6	1				6	25
	3		1	3		4		1				2	7
	4												2
	5	10						1					
	6	2						1					1
	7	16						1				1	4
	8	2										1	2
	9	7						5				2	2
	10	12				2			2	2			
NORTH-ARM	1			9		14	12	3			18	2	
	2			4		22			2		2		
	3	5	1	1				1					
	4												
	5												
	6	11		1							1		1
	7	6										3	4
	8	11						1					
	9			3									
	10	1		25		52			3		1		
DAM	1			1			1		1			3	
	2	4										1	
	3	10										2	
	4	3											
	5	12					1						2
	6	9											
	7											1	
	8											1	
	9			9	4	4			1			6	3
	10			13								1	
TOWER	1	6						2					
	2	13						1				1	
	3	10										3	
	4	18					2	1				4	1
	5	17		1				7				3	3
	6	19					1					1	1
	7												
	8	6				1			1	1			1
	9			7		3					1		
	10	3		19		2	2	19			4	3	7

Date: 13.12.76

Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
SOUTH-ARM	1												
	2						10					34	
	3						8			1		21	
	4	1					9	1		2		20	
	5												
	6	1						1			1	1	
	7	3					2						
	8	2					4			1	3		
	9	8					1				9	1	
	10	5									1		
NORTH-ARM	1						1						
	2		4				1						
	3	8					1				1	1	1
	4	3									1		2
	5	7									1		
	6	1					15				1		
	7												
	8												
	9												
	10												
DAM	1						31				1	28	
	2												
	3	9					2					19	
	4	2					2					17	
	5	12					10					35	
	6	6					2				1	16	1
	7	10					1	1				15	1
	8	2										2	
	9												
	10						2						
TOWER	1	2					15					3	
	2	5					16					1	2
	3	1										1	
	4	21					3				1		1
	5	2										3	
	6	2									1	3	
	7										1	16	
	8									1		4	
	9	1											
	10						1						

Date: 28.11.77

Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
SOUTH-ARM	1	1							5			7	
	2								3				
	3											2	
	4						9					8	
	5	1					9					6	1
	6	1					1					1	11
	7	2					13					3	
	8	7					10					7	
	9	5					28					10	1
	10	6					12					23	
	11											18	2
	12	1										3	
NORTH-ARM	1								2				
	2						1					21	
	3						2						
	4						1						
	5												
	6											2	
	7	2					18					10	2
	8	2					4					7	5
	9	1					11					1	
	10	2										1	
	11						3						
	12	1								1		2	
DAM	1					3	2					11	
	2						9					15	
	3						1			1		20	2
	4						1						
	5	5					10		1			4	2
	6	4				1	3		6			3	2
	7	4					23					4	2
	8	2					3					1	1
	9	6					20					7	1
	10	4					14					3	1
	11	6					4					7	1
	12			1		2					1	14	1
TOWER	1	7					2					2	1
	2	8					42					9	
	3	1					7					6	
	4						1					2	
	5						1					1	
	6												
	7						1					3	1
	8												
	9	1					1		1			9	2
	10						1		5				1

Date: 13.1.78

Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
SOUTH-ARM	1	1							2	1	4	45	5
	2	10				2	4		3		3	44	2
	3	1							1			6	5
	4	1					7				1	10	5
	5	8					11					11	1
	6	2									1	6	20
	7	5										5	7
	8	3					12					9	1
	9	6					16					5	1
	10	11					7					12	2
	11	11					14					23	33
	12	1							1			3	
NORTH-ARM	1							5		3		75	1
	2	1					2					47	3
	3						1				1	12	3
	4						7					9	
	5	1										3	
	6	2				1						3	3
	7	4					23					6	5
	8	1					9					2	2
	9	6					5					4	4
	10	1											
	11					4						9	3
	12												
DAM	1	28				5	10					22	34
	2	4				1			1				14
	3	7					4					12	12
	4	5				1	3					9	1
	5	3					3						
	6	15					17		1			2	17
	7	7					7				1		1
	8	6				1	22			1		2	1
	9	5					11					7	8
	10	3					6				1	6	1
	11												4
	12						1						2
TOWER	1	1							1	1	1	6	2
	2						1				1		
	3						3				1	2	
	4	2					10					1	
	5	1										3	
	6	1					8					21	2
	7	1										5	1
	8	2					11					2	1
	9	9					30				1	21	10
	10						15					6	4

Date: 23.2.78

Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
SOUTH-ARM	1			1	3	3						.8	2
	2					1			1			16	1
	3	2					1					1	10
	4	1					11					14	5
	5										4	4	9
	6	10										24	15
	7	11					19					6	
	8	6					24				1	12	4
	9	1					14					8	2
	10						33					2	3
	11	2					3					49	3
	12	7									2	23	6
NORTH-ARM	1	3							6			2	2
	2	15					3	1	3				17
	3	1										3	
	4												
	5						2					1	
	6												
	7	3											
	8						7				1	5	7
	9	10					27					5	27
	10												
	11											1	
	12	1				3	1					2	
DAM	1			2								3	
	2	12					10						16
	3	2					7						1
	4	4					3						2
	5												
	6	3					6						4
	7	4					2						3
	8												
	9	19					26					6	26
	10	2					7					2	5
	11	2					2					1	12
	12	4							1			1	16
TOWER	1	3							1			26	1
	2	2					10				1	24	
	3	1					5					9	
	4						2					2	
	5						2					2	
	6						2						
	7	2					1				1	4	2
	8						1					4	
	9	4					23					10	11
	10	2					2					15	24

Date: 30.3.78

Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
SOUTH-ARM	1								4			1	
	2	1				2	1		2			10	
	3	1					1		4			2	3
	4						1						2
	5						2					2	3
	6											1	
	7	2										12	15
	8						1			1	2		2
	9	2					10					8	5
	10	4					4					10	2
	11	2					4					3	3
	12						1					1	
NORTH-ARM	1						2		6			5	
	2	1							1			13	
	3								2			2	
	4						2					14	1
	5					1	11					5	6
	6	3					21					4	21
	7	6					8					2	3
	8						1		2				
	9						4					2	2
	10						1						
	11					2			1			2	
	12				1	7	1		1				18
DAM	1				2		2					5	1
	2						1	1				5	2
	3	2		1								2	4
	4	10					6						23
	5	4					3						10
	6	8					2		1			1	17
	7	5					11						23
	8	5					17					1	9
	9	1					1					3	8
	10	4					4				1	4	15
	11	4					2				1	1	21
	12	11			1	1			9			9	20
TOWER	1	1							1		2	18	4
	2						1					8	6
	3						2					4	
	4						1					1	
	5						4					3	1
	6						1				1		
	7	3											1
	8	1					4					5	3
	9						11						7
	10	2					4					21	31

Date: 17.4.78

Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
SOUTH-ARM	1	1		37	1	1						1	
	2			1		1				1		6	11
	3								1				
	4	3					6					1	10
	5						1						1
	6	2			1		5					12	13
	7	4		1								1	23
	8	7		1					1			6	46
	9	6										5	29
	10	10					4					7	5
	11	6					27					6	17
NORTH-ARM	12						1		2			15	3
	1			6									
	2												
	3	2					1		10			8	3
	4								1			3	
	5	2					13		1			3	2
	6								4			4	
	7	9					15				2	3	40
	8	9					23					4	18
	9	3					16					2	4
	10												
DAM	11								1			6	1
	12			1								7	2
	1			2		2							
	2	1		27	1	2			1			11	3
	3			9		2	3				1	21	3
	4					1			8			3	
	5								1			1	2
	6	7					12		1				36
	7	9					11		1				35
	8	16					3					3	73
	9	3					1						8
	10	11					3						17
TOWER	11												
	12	9					3		1				14
	1			2		4			3			5	12
	2	3							10			29	10
	3	2					16		1			54	6
	4	3					21					16	8
	5	1					7						3
	6						2						
	7						2					5	
	8	2					40					14	38
	9	4					4					5	8
	10	5					1					6	3

Date: 17.5.78

Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
SOUTH-ARM	1	1		1			1		10			3	1
	2			10	3			1	3			1	2
	3								1				3
	4	2											9
	5	2					4					8	5
	6	3					8		3			1	7
	7	2					4		1			2	11
	8	6					12					3	7
	9	20					8					10	11
	10	6					21					1	20
	11	2										3	1
NORTH-ARM	12						1		1			4	1
	1	1		1					12				1
	2								15				
	3	1					1		4			5	1
	4	1					1		1			7	5
	5						1		1			2	6
	6										1	2	2
	7	4							1			1	16
	8								1				8
	9	7					1					3	10
	10	3					3		2				11
	11	3											
DAM	12		3						8			2	4
	1								1				2
	2			2			1		3				3
	3						9		2				2
	4	3					3					3	8
	5	4					3						12
	6	11										1	33
	7	3					2		1				3
	8	5					4						17
	9	1											1
	10	5					17					4	17
	11	1					24					1	1
TOWER	12								12	1		1	
	1			1	2				1			1	1
	2								4			1	
	3						21		1	1		7	1
	4	2					24					11	2
	5											10	
	6	1					2		1			2	
	7	2					111					2	2
	8						1					1	
	9	1										1	2
	10						4					3	6

Date: 19.6.78

Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladus	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
SOUTH-ARM	1				1		2					1	1
	2			1		15							1
	3												3
	4	7										1	
	5	1											
	6											1	
	7	4											
	8												
	9	13										2	
	10	9										1	1
	11	13					9						
	12												
NORTH-ARM	1					2			1				1
	2	2											1
	3						6						
	4												
	5	1											
	6	3					2					1	1
	7						3						
	8	6					14					1	
	9	2					11						
	10	4					6						
	11	1											
	12					7							16
DAM	1			1		2						1	9
	2												
	3						6						75
	4	11											6
	5	13					3						
	6	3					1						3
	7	4					1					1	1
	8	2					3					1	
	9	3					3						
	10	8					4						
	11	5					3					1	
	12			2		3			1			1	8
TOWER	1			12		21		1	1				
	2	1											
	3												
	4	2										2	
	5											3	
	6	5										2	
	7	5										1	
	8												
	9						2						
	10	6					4						1

Date: 25.7.78

Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladus	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
SOUTH-ARM	1						1				13	1	1
	2												1
	3												1
	4	1											1
	5												
	6												
	7	3					1					1	1
	8						3						
	9	7					3					1	
	10	7					1						1
	11	1											
NORTH-ARM	12		1								3	2	
	1	1	1						2				
	2												
	3												
	4						1						
	5	5					1						
	6	5											
	7	4										1	
	8												
	9												
	10												
	11												
DAM	12					2	1		1			1	2
	1		2	3	7	3			3				4
	2				1		1				1		
	3												
	4	3					1				1		4
	5	11					1	1				1	41
	6	17		3									21
	7	7		1			1						4
	8	3		1									2
	9	21		3		1	1					1	9
	10												
	11												
TOWER	12			6	1	1			1				3
	1		4			1	1						
	2												
	3	3											2
	4	1					1						
	5												
	6	1											
	7												
	8	3											1
	9	2					2						2
	10	9					1					1	1

[illegible]

Date: 23.10.78

Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
SOUTH-ARM	1										2	1	
	2									1	4	3	
	3									1	4	2	
	4											1	
	5											1	
	6											1	
	7											3	
	8	3									3	3	2
	9												
	10	3					1						
	11											1	
	12												
NORTH-ARM	1												
	2												
	3												
	4											3	
	5												
	6	1										8	
	7										1		
	8												1
	9												
	10										3		
	11												
	12								1				
DAM	1												
	2						1	1				1	1
	3						1				1	1	
	4										2		
	5	3									1		
	6												
	7	3									1		1
	8												
	9	7						1				3	
	10	3											
	11	4									1		
	12										4	1	4
TOWER	1						1						
	2	2										1	
	3												
	4												
	5										3	5	
	6	5					3				3	3	1
	7						3					3	1
	8										1		
	9	1					1				1		
	10	11	1				1				2		1

[illegible]

APPENDIX C Chironomid larvae in van Veen grab samples, transects
2NA and 2SA

Date	Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
12.5.77	SECOND SOUTH-ARM	1												
		2	2											
		3	1											
		4												
		5						1						
		6	1			1		3						
		7												
		8	1											
		9	2											1
		10				1		1						
12.5.77	SECOND NORTH-ARM	1				7								
		2	11			6								1
		3				6								
		4	2			1								1
		5												
		6												
		7												
		8	2											
		9				4								
		10				2								2
26.5.77	SECOND SOUTH-ARM	1												
		2												
		3												
		4		1										
		5	1											
		6								1				
		7												
		8	1											
		9												
		10	2											1
26.5.77	SECOND NORTH-ARM	1												
		2		1		2		4						1
		3						1						1
		4						1						
		5												
		6												
		7						1						1
		8												
		9	3			5								
		10				4								

Date	Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
20.6.77	SECOND SOUTH-ARM	1				1	1							
		2				1		1						
		3						1						
		4	1											
		5												
		6												
		7												
		8						1						1
		9	1											
		10			2							1		
20.6.77	SECOND NORTH-ARM	1	3		118	42	3	17	3		1			26
		2	55		1	22	4	13						78
		3	4		1		3	3	2					15
		4			1	1	10	6	1					3
		5						1						
		6			1									2
		7					1							3
		8						13						1
		9	1				4	7						
		10	4		45	1	4	18						3
11.7.77	SECOND SOUTH-ARM	1	5					1						
		2			5		7	1		2				
		3			3		1			1				
		4	6											1
		5						2		1				
		6	1					1						6
		7						9						
		8	10		3		1	9						19
		9	5					9			1		1	1
		10	7		21		8	44		1			1	86
11.7.77	SECOND NORTH-ARM	1	80		12		24	29	1					139
		2			9		6	1	2					
		3	14		1		2	1		1			1	3
		4	22				3	111		1				7
		5	9					10						1
		6	1		3			4						1
		7						2					1	
		8	14		1		3	4					2	3
		9	5				27	22		1	1			10
		10	17		6		28	16	1					66

Date	Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
31.8.77	SECOND SOUTH-ARM	1			3		2	132	24	5			5	
		2	2	1	3		3	43	25	2			5	
		3	7					4					2	14
		4	7				1	27	4	1			4	12
		5						18						3
		6	2					11						7
		7	2					20	1	3		2	3	8
		8	2					6					6	46
		9	8					26		1			3	12
		10		6	6		5	1		3			1	
31.8.77	SECOND NORTH-ARM	1	7	5	33		59	18	5				1	12
		2	5		4		9	5	8					
		3	8	2	10		8	31	29	34				3
		4	10					26		3			10	22
		5	44					13	2	1	2		11	362
		6	4	1				15					8	16
		7	10				2	20	8	8			12	141
		8	17				2	16	2				2	4
		9	11	3	2		43	16	8	3				
		10	20		6		2	8	3	1			1	13
26.9.77	SECOND SOUTH-ARM	1			3			14		1	1	1	17	3
		2			1			4		1			3	
		3	1					18		9			3	
		4	30					2		1			2	7
		5	4					11						
		6	48					5					9	3
		7	39					5	1				21	2
		8	13					9		3			9	
		9	2				3	12		5			4	
		10					1	3						
26.9.77	SECOND NORTH-ARM	1	2	8	37		128	173	1	13	3		4	7
		2	1				2	18		1			1	21
		3	11		2			55		2	1		10	129
		4	7	1			2	123		4				
		5	36					4					5	10
		6	50					3						28
		7	52				1			14	1		6	22
		8	29					1		2	1		13	17
		9		4			38	10		2				
		10	4		1		1	13				1		

Date	Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
24.10.77	SECOND SOUTH-ARM	1	2				25	106	4			1	39	46
		2	1					9					15	28
		3	43					9		2			22	14
		4	22					6					8	56
		5	57					10	1				17	20
		6	24					2					2	13
		7	42					9					20	9
		8	75					2					21	12
		9	3					1		2	1	7	13	
		10			13		15	4					80	1
24.10.77	SECOND NORTH-ARM	1	19				31	43	1					4
		2	12				14	19	1	4			8	35
		3	2				14	8		6			11	93
		4	1							1				
		5	27				1						4	
		6	29					7					10	50
		7	38										1	16
		8	18	1				2		3			1	
		9					8	3		3			1	
		10	14		1		75	31		1		2	1	9
29.11.77	SECOND SOUTH-ARM	1	1				53	7	2				84	488
		2	1				10							14
		3	20				1	7					8	33
		4	45					11				1	7	14
		5	51					11	1				22	45
		6	41					14					19	45
		7	13					6			1		23	25
		8	41					6					45	4
		9	69				2	4	1			2	56	10
		10			1		15	2	1	1			44	
29.11.77	SECOND NORTH-ARM	1	57				105	145	1	1	1	7	90	52
		2	20				120	41				1	12	16
		3	3				7	11		1				
		4	22					4		1			6	4
		5	54					2					7	3
		6	37										2	27
		7	6										1	5
		8	23				1	2					1	1
		9	3				80	1		2			1	8
		10	2		5		32	1					2	8

Date	Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
16.1.78	SECOND SOUTH-ARM	1						4						
		2	1				1	8					2	4
		3	39				1						1	13
		4	58					10			1		6	57
		5	64					15					9	53
		6	42					9					8	10
		7	42				2	2	1	1			17	24
		8	73				6	3	3				30	26
		9	86				34	60	1	14	3		115	45
		10												
16.1.78	SECOND NORTH-ARM	1					15	11					8	7
		2	9				15	9		3		1	10	5
		3	17				6	9		8			2	
		4	24					33					12	21
		5	28					1					9	47
		6	38				1						1	47
		7	16											7
		8	2				4	1						
		9	4		2		47	2					2	142
		10	1		1	6	3							1
28.2.78	SECOND SOUTH-ARM	1						19	3				81	3
		2	1				54						1	6
		3	86					6					11	23
		4	30			1	1	20					16	31
		5	36				2	2					8	166
		6	48				2	4					9	25
		7	53			1	2						23	68
		8	94			3	8	3					41	58
		9	7			3	9	3			2		6	2
		10			4	2	17	4	3				14	1
28.2.78	SECOND NORTH-ARM	1			1	22	1							1
		2	8				25	31			3		17	14
		3	1	1			43	4		2			3	
		4	10				4			2				3
		5	35					3					2	81
		6												
		7	35				4					3	5	38
		8	1				23	1						
		9	4		1		50	4	1		1	2	5	68
		10				2								1

Date	Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladus	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
16.3.78	SECOND SOUTH-ARM	1	4		3	7	17	9				1	32	27
		2	20				1	13	1	1			38	39
		3	94				3	18		1		1	10	57
		4	53			2	4	2					8	46
		5	16			3	1	11					19	50
		6	6										5	2
		7	42			4	2	3					7	49
		8	21					1		1			11	24
		9	15			3	17	19		5			98	98
		10			20	25	36	1	3		3		58	16
16.3.78	SECOND NORTH-ARM	1				10	4							2
		2	79				129	63	1	4			39	387
		3	87				27	1	3			1	3	4
		4	6			2	46	15		5			4	15
		5	16					3		1				8
		6	79					9					6	108
		7	39				1							73
		8	11					8					1	
		9	2			10	14							22
		10	1			2	1							
12.4.78	SECOND SOUTH-ARM	1	6		5		8	1	4	2			26	74
		2	57	1	1	2	27	30		13			67	196
		3	53				1	10		1			4	27
		4	44					3		2			10	23
		5	61			2	5	10	2	1			20	149
		6	21										18	43
		7	23					2		1			10	107
		8	102			1		10		2			26	129
		9	65				6	6		2			52	75
		10	34	2	43	6	31	13	1	11			129	104
12.4.78	SECOND NORTH-ARM	1				12	1			1				1
		2	5				19	8		5			14	35
		3	66				32	6		6		1	12	20
		4					13	1		9				
		5	35				2	8		1			3	71
		6	3					1		2		1	1	17
		7	48	1			2	2		2			6	130
		8	48	1			3	2		4			7	87
		9	2				1			7				1
		10	1			7								

Date	Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
17.5.78	SECOND SOUTH-ARM	1	6	10	2	3			2	1				16
		2	10	3		1		3	2	10			5	63
		3	39					18	1	2			9	46
		4	61					2		1			2	140
		5	79					7					5	36
		6	72					9		1			3	25
		7	45					1						25
		8	67					3					1	24
		9	7					6		3				2
		10												
17.5.78	SECOND NORTH-ARM	1	5	4		2		1	6	2			1	9
		2	42	1				1	1		2			4
		3	30				1	2		5	2	3	7	45
		4		1			3	1		16				
		5	26					14					1	11
		6	1					1						
		7	4											5
		8	11	3				2					2	62
		9	2				2	6		4				2
		10	2			14	1		4					
13.6.78	SECOND SOUTH-ARM	1	18										3	5
		2	66										1	6
		3	40											
		4	24											
		5	66										5	
		6	30					1	1		1		1	
		7	54					2	1	1			7	
		8	55										2	
		9	57					1					4	
		10	96		52		340		16				20	608
13.6.78	SECOND NORTH-ARM	1					112	4						524
		2	4				20	4	1					23
		3	15				21	13					6	121
		4	5				6							2
		5					1							
		6	19					2						
		7	26				1	1	1		1			3
		8	11											
		9					14							
		10	3	3			77							

Date	Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
10.7.78	SECOND SOUTH-ARM	1					13	9	5	3			3	
		2	1		3	21	42	35	6	3		4	30	
		3	1				4	8					4	1
		4	13				3	1					1	108
		5	15										2	127
		6	26											118
		7	5					1					3	15
		8	29					1					6	109
		9	59				1					1	3	153
		10	4				56	5				2	66	18
10.7.78	SECOND NORTH-ARM	1		16	44		180	4	16	4		8	8	8
		2	2		2	3	12							5
		3					2	1						
		4												
		5	8					1						1
		6	9									2		11
		7		1				4					1	28
		8	26				1	1		1				22
		9				3	24							
		10			40	12	208							
17.8.78	SECOND SOUTH-ARM	1	3	1			36	4	1	1			1	
		2					1	1						2
		3	1									1	3	69
		4	10											59
		5	16										2	7
		6	6									1	6	17
		7	13									1	4	76
		8	2				4						10	13
		9		1										
		10												
17.8.78	SECOND NORTH-ARM	1					21							
		2												
		3	3											
		4	3					1						2
		5												3
		6										1		20
		7	4											
		8												
		9						2						
		10	24				229	5		1				

Date	Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladus	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
19.9.78	SECOND SOUTH-ARM	1						12						
		2	23					1	2			1		32
		3	3									1		20
		4	14									1	1	4
		5	12					2				2		5
		6	12					2						9
		7	5						2				5	1
		8	1											2
		9												
		10	2											
19.9.78	SECOND NORTH-ARM	1		1	3		9							
		2		1			2							
		3	11											1
		4	1											
		5	3						2				2	
		6											1	5
		7	6									1	1	4
		8												
		9						4						
		10	7	29			14	17	1		1	5	1	2
23.10.78	SECOND SOUTH-ARM	1	1				2	7	1			8	7	7
		2						6				2	3	13
		3	2					1				3	1	3
		4	8					1	2				1	
		5	17					1					1	2
		6	12									4	10	1
		7	10										4	
		8	6					3					19	67
		9	3					10					34	6
		10												
23.10.78	SECOND NORTH-ARM	1	2	2			16							
		2		6				1						
		3						8						
		4						1						
		5	9										2	2
		6	1											1
		7												
		8						1						
		9		3			1							
		10	4	108			28	44						

Date	Transect	Grab Number	Procladius	Ablabesmyia	Cricotopus	Orthocladius	Psectrocladius	Chironomus	Cryptochironomus	Endochironomus	Glyptotendipes	Microtendipes	Polypedilum	Tanytarsini
19.4.79	SECOND SOUTH-ARM	1					1							1
		2	16					3				2	4	75
		3	13									1	3	27
		4	32									1	1	7
		5	31						1			7	9	52
		6	11									8	5	39
		7	20									3	5	12
		8	6						2			5	9	126
		9			1		1							1
		10			6									1
19.4.79	SECOND NORTH-ARM	1	2											2
		2	5					1					7	26
		3	3											
		4	20									10	4	15
		5	5									2	1	
		6												
		7	1											
		8						1						
		9	3				1	1					1	
		10	2		1		4	1				1		

Date: '29.7.77

Fish Number	Species	Procladius		Ablabesmyia		Cricotopus		Orthocladus		Psectrocladius		Chironomus		Cryptochironomus		Endochironomus		Glyptotendipes		Microtendipes		Polypedilum		Tanytarsini	
		L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P
1	B		4							50	31	161				3				1				2	
2	B	4	4																					8	
3	B		1					2		4		26								1				9	
4	B	5	3							4		41												14	
5	B											11													
6	B									3	4	1			1	3									
7	B		1							28		3				3									
8	R				14	6				3	115	1	1		1	6								1	
9	R																								
10	R		1			2				11		4				2									
11	R		2			5				30		18				1								3	
12	B		2			4				28		29												4	
13	R	3	65			2	7	3	326	33		2			2	4								4	
14	R	2	156			5	1	1	205	56		2	1		2	1								6	
15	R		1		5		1			3	7	5			2									3	
16	R	1	5	1			2	2		11	24	1			1									1	
17	R	2	18			9	1			199	13				1	1									
18	R		2			1				4	2	1		4									1	2	
19	B		21							1		19			1									46	
20	R						1			4	1	1			2									1	
21	B		1									5	5									1		1	
22	B	2						6				8												81	
23	B		2									1	290			2						4		7	
24	B		12							4		35	2	82										35	
25	B					1				1															
26	B																								
27	B									1		1												2	
28	B		6		1			2		1		8		5										100	
29	B											27		5										17	
30	B									1		16		2				1						33	
31	B		4			2		1		2		17												62	
32	B		8									26		1										21	
33	B		3					1				3				1								12	
34	B																								
35	R																								
36	B		1					1	1	1	6	169	4		1					1	1	1	12	2	
37	B									12		35												49	
38	B		1							1	2	21												19	
39	B							2		1		3												1	
40	B									2				32			1							4	

Date: 13.8.77

Fish Number	Species	Procladius		Ablabesmyia		Cricotopus		Orthocladius		Psectrocladius		Chironomus		Cryptochironomus		Endochironomus		Glyptotendipes		Microtendipes		Polypedilum		Tanytarsini	
		L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P
1	B	4	1			12						10												64	
2	B	283	11			28				8	2	26	8		1		2					3		116	
3	R	1	3			1				2	2		4		12	1						9	3	6	
4	R	5	9			49	2			13	64	1	2		51	8						27	9	6	40
5	R	2	5			4					6	7										1		1	
6	R		32			15				1	26	4	1		1	1								9	
7	R	1	41			8	24			4	40	1	5	10		9	4					2		109	
8	R	1	37				2			1	26	7			1	3							1		32
9	R	1	39							11	19	2	5		1	1									11
10	R		4			2	4				25	1			3	2									83
11	R		20			1	1				11	2				1						1			29
12	R	3	52			1		2		5	29	3	63			5									12
13	R	8	2				1			10	14	13	62	1									2		2
14	R	1	110				8			7	71		10												35
15	R	5	2							1		25				1						1			1
16	R		6								1	23				2									
17	B	3	30							1	1	231				2									2
18	R									17	1	3	1												
19	R		37								1	17													
20	R																								
21	B	12	129							33	13	27	60		38		1				18				
22	B	4	16							2		51	4			2					2			1	
23	B	1	1							2			9		12						2				
24	B	4	15				2			27	6	3	5	33	25	1					8			1	
25	R	15	20							2	7												15		
26	R		17			5	4			2	35	3	2			1							4		
27	R	13	40			4	1			78	51	1	10	109	83	2	2			1		14		38	
28	R	2	39				1			188	7	3	32	9	2	16									10
29	R		19				1				7					17							1		8
30	R		48							8	26	8	2		36	16									22
31	R		27							3	3	5	1			2									7
32	R	3	38				2			36	15	3	3		37	14						3			1
33	R	2	2				2					2	1			9									2
34	R	1	6			1				5	1	3	2		5	6						3			2
35	R		11			1	12			1	16		1			34									9
36	R	2	7			1				26	1				68	10									2
37	R		5				1			1	8	1			104	23									8
38	R		161			2	1			62	14	4	4		20	35									4
39	R	1	5			2				7	26	1	3		1	7						3			11

Date: 27.8.77

Fish Number	Species	Procladius		Ablabesmyia		Cricotopus		Orthocladus		Psectrocladius		Chironomus		Cryptochironomus		Endochironomus		Glyptotendipes		Microtendipes		Polypedilum		Tanytarsini	
		L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P
1	R	1	17			5				17	3	2	1	82	3							1		1	
2	B											3													
3	R	1	44			6				6	21		1	17	13								2	15	
4	R		23			14	9			13	8	2	2	14	12								2	7	
5	R	3				5				5			1	6									1		
6	R	11	28			74	25			18	27	7	1	1	11							12	17	13	
7	B	1	2				3				1	4												3	
8	B	1	12													3	94							9	
9	R	1	39			1	1			5	3	40	2	7	59							8		59	
10	R						1			2	2	1	6	1	25							2		15	
11	B		16									2		4	12									1	
12	R	11	50			5	4			24	8	33	12	102	89							19		65	
13	B	1	63							1		2	1	2	28									1	
14	R	1	34				1			5	1	12	8	13	5									11	
15	R	9	1			4				14	4	8	19	6	3	9						1		9	
16	R	1								4			4	25											
17	R	5	40			1	3			9	5	25	19	37	37							1		5	
18	R		4	1						1	1	10	3	1	32							3		21	
19	R											15			9										
20	R	59				1				7	24		6	5								1			
21	R						3			4	6	6		12	2									9	
22	R									2		3	2												
23	R		77				1				6	192											2	154	
24	B											3				83									
25	B										5	76				1									
26	R		96								3	4				1								38	
27	R	2	8			1				1	1	1	1	54	32										
28	B											9	1	9	33										
29	B		1								41	246		1	19							1		1	
30	B	4	4							1	102	430	1		40									4	
31	R	2	3	2						6	3	3	4		3							2		6	
32	R	16	1			2				6				5	2							2			
33	R	31	8			6				11		1	1	66	1							1	1	1	
34	R		4			1				4			1	45											
35	R															1								1	
36	R	55	2							8		1		22	6										
37	R		2							7		1	1	15											
38	R		14							6	8			1	8							1		3	
39	R										1			1	1										
40	B	5	3									12	28	7	1	10						1		4	

Date: 10.9.77

Fish Number	Species	Procladius		Ablabesmyia		Cricotopus		Orthocladius		Psectrocladius		Chironomus		Cryptochironomus		Endochironomus		Glyptotendipes		Microtendipes		Polypedilum		Tanytarsini	
		L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P
1	B																								
2	R					1				3	3	3	2			2								12	
3	R		1		11	2	1			140	23	4	8			5	18					2		522	
4	R																								
5	R		1								6					14								1	
6	B										1	12	30			6								4	
7	R									6				1											
8	R																								
9	B		11								5	1	2	2										1	
10	B									6				4											
11	B									1															
12	B		1							3				1		1									
13	B		17							2				4		1									
14	B																								
15	B																								
16	B									1															
17	B																								
18	B		1	48								8	1											3	
19	B		4	32							6					1								5	
20	B											3				27								95	
21	R		61	146						5		28				17						20		72	
22	R																								
23	R															2									
24	B											193				16									
25	R		4	2						7	16	41	2			28	80							34	
26	R		2	6						1	12	1	140			32	95							83	
27	B			9								178													
28	B			13						3		40	3		1							3		7	
29	R											4				1								6	
30	R			23						3		89	2			1						1		20	

Date: 28.4.78

Fish Number	Species	Procladius		Ablabesmyia		Cricotopus		Orthocladus		Psectrocladius		Chironomus		Cryptochironomus		Endochironomus		Glyptotendipes		Microtendipes		Polypedilum		Tanytarsini	
		L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P
1 R		12								1	4	73				9		1		1				2	
2 B		7								2	10	7				10		1							
3 R		1									25	25				2									
4 R		1								7	92	22				34				2	6			10	
5 R		3								7	23	12				21		2		1	6			1	
6 R											1					26		1			2				
7 R		1						2		2	5					28					2				
8 R		1						2	1		3	5				12		1		2	2				
9 R		14				1		6		3						82		5			2				
10 R		23						7		14	3					35		8		2	1				
11 R																14		5			1				
12 R		4						3		3	8	3				38		9		3	4			10	
13 B		2							2	3	32	3	4			11				82			1	12	
14 R		3	1					5		6	6	1				16		6		17	1			16	
15 R											33	46								211				91	
16 R								1								19		1							
17 R											5	6								5				44	
18 R		12						5		1	1	24				6				16				4	
19 R										1		1													
20 R								1			6	22				30				12				320	
21 R		3						4	1	4	1	4				24				3	1			202	
22 B		1										2				1		1		2					
23 B		1									1					9									
24 B		3									1	4				5				7				1	
25 R						2	1	1	2	32		16				3				22				20	
26 B		9						1			14	45				22		1				1		3	
27 R										2	1	5	3			7						5			
28 R											1					4									
29 R									4		52	32								38				520	
30 R									4		136	24								44				204	
31 R						1					4									10				6	
32 R		12	1					4		28	128	44				50				36	3		2	428	
33 R		3						4	8	11	368	32				26		1		372	6			72	
34 R		132	1						1	16	26	12				60		20		194	364	4		17	
35 R		2				8		182		2	17	4				3		1		7				30	
36 R		2						1		11	144	448				1				80				148	
37 R											45	100								1				31	
38 R						8		34			111	64								9				1	
39 R		8				2		3		7	54	134				39		11		14			2	36	
40 R		4								10	34	80				10				34			2	131	
41 R								1	5	1	5	47	61			1				1				38	

Date: 9.9.78

Fish Number	Species	Procladius		Ablabesmyia		Cricotopus		Orthocladius		Psectrocladius		Chironomus		Cryptochironomus		Endochironomus		Glyptotendipes		Microtendipes		Polypedilum		Tanytarsini	
		L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P	L	P
1	R		2			3				86					1										
2	R		10			1				5															
3	R		96							5	6														

4-19 No Chironomids

Date: 23.9.78

1	R	3	7																						
2	R		12																						
3	R		1																1						
4	R		21							2	2														6

5-20 No Chironomids

Date: 7.10.78

1	R	1						1						1											1
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2-20 No Chironomids

Date: 21.10.78

1	R																								133
2	R							1		1															1
3	R																								35

4-19 No Chironomids